MOLTENO FERNS:
Late Triassic biodiversity in southern Africa

Heidi M Anderson & John M Anderson
Molteno ferns: Late Triassic biodiversity in southern Africa

by

Heidi M. Anderson and John M. Anderson

Pretoria

2008
This series has replaced Memoirs of the Botanical Survey of South Africa and Annals of Kirstenbosch Botanic Gardens which were inherited from predecessor organisations.

The plant genus *Strelitzia* occurs naturally in the eastern parts of southern Africa. It comprises three arborescent species, known as wild bananas, and two acaulescent species, known as crane flowers or bird-of-paradise flowers. The logo of the South African National Biodiversity Institute is based on the striking inflorescence of *Strelitzia reginae*, a native of the Eastern Cape and KwaZulu-Natal that has become a garden favourite worldwide. It symbolises the commitment of the Institute to promote the sustainable use, conservation, appreciation and enjoyment of the exceptionally rich biodiversity of South Africa, for the benefit of all people.

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**Citation of this publication:**

## CONTENTS

<table>
<thead>
<tr>
<th>Section</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>FOREWORD</td>
<td>iv</td>
</tr>
<tr>
<td>PREFACES</td>
<td>v</td>
</tr>
<tr>
<td>ABSTRACT</td>
<td>vi</td>
</tr>
<tr>
<td>ACKNOWLEDGEMENTS</td>
<td>vii</td>
</tr>
<tr>
<td><strong>MOLTENO FERN BIODIVERSITY &amp; RELATED TOPICS</strong></td>
<td></td>
</tr>
<tr>
<td>1. INTRODUCTION</td>
<td>2</td>
</tr>
<tr>
<td>2. SAMPLING</td>
<td>2</td>
</tr>
<tr>
<td>3. FREQUENCY &amp; ABUNDANCE</td>
<td>2</td>
</tr>
<tr>
<td>4. AFFILIATED ORGANS</td>
<td>2</td>
</tr>
<tr>
<td>5. MEASURING BIODIVERSITY</td>
<td>3</td>
</tr>
<tr>
<td>6. PROMINENCE (COLONISATION SUCCESS)</td>
<td>3</td>
</tr>
<tr>
<td>7. MOLTENO BIOME &amp; HABITATS</td>
<td>3</td>
</tr>
<tr>
<td>8. FORMAT OF THE SYSTEMATICS SECTION</td>
<td>3</td>
</tr>
<tr>
<td>9. FERN CUTICLES</td>
<td>4</td>
</tr>
<tr>
<td>10. CLASSIFICATION OF MOLTENO FRNS</td>
<td>10</td>
</tr>
<tr>
<td>11. TABLES 1–11</td>
<td>5–29</td>
</tr>
<tr>
<td><strong>SYSTEMATICS OF THE MOLTENO FRNS</strong></td>
<td></td>
</tr>
<tr>
<td>Marattiales (fertile)</td>
<td>32</td>
</tr>
<tr>
<td>Marattiaceae</td>
<td>32</td>
</tr>
<tr>
<td>Drepanozamites</td>
<td>32</td>
</tr>
<tr>
<td>Asterothecaceae</td>
<td>38</td>
</tr>
<tr>
<td>Asterotheca</td>
<td>38</td>
</tr>
<tr>
<td>Osmundales (fertile)</td>
<td>46</td>
</tr>
<tr>
<td>Osmundaceae</td>
<td>46</td>
</tr>
<tr>
<td>Osmundopsis</td>
<td>46</td>
</tr>
<tr>
<td>Rooitodites</td>
<td>52</td>
</tr>
<tr>
<td>Birtodites</td>
<td>72</td>
</tr>
<tr>
<td>Elantodites</td>
<td>82</td>
</tr>
<tr>
<td>Osmundales (sterile)</td>
<td>130</td>
</tr>
<tr>
<td>Cladophlebis</td>
<td>130</td>
</tr>
<tr>
<td>Sphenopteris</td>
<td>162</td>
</tr>
<tr>
<td>Birmolitia</td>
<td>166</td>
</tr>
<tr>
<td>Nymbopoterum</td>
<td>170</td>
</tr>
<tr>
<td>Parsorophyllum</td>
<td>174</td>
</tr>
<tr>
<td>Stormbergia</td>
<td>181</td>
</tr>
<tr>
<td>Polypodiales (sterile)</td>
<td>184</td>
</tr>
<tr>
<td>Nymboidiantum</td>
<td>184</td>
</tr>
<tr>
<td>Displinites</td>
<td>192</td>
</tr>
<tr>
<td>Molteniella</td>
<td>196</td>
</tr>
<tr>
<td><strong>MOLTENO FERTILE FRNS, COLOUR PLATES</strong></td>
<td>199</td>
</tr>
<tr>
<td><strong>BIBLIOGRAPHY</strong></td>
<td>254</td>
</tr>
<tr>
<td><strong>GLOSSARY</strong></td>
<td>257</td>
</tr>
<tr>
<td><strong>INDEX</strong></td>
<td>258</td>
</tr>
</tbody>
</table>
John and Heidi’s ‘Molteno Monographs’, as I have come to call them, represent one of very few current examples of ongoing research with monographic treatment of all the plant fossils in a given geological unit. Indeed, as I write, I am not aware of any other comparable series. The Molteno Monographs are truly remarkable for the in-depth coverage, for their detailed documentation of a fantastic collection of plant fossils and for the sheer hard work and determination shown by the authors over a lifetime devoted to this task. These volumes are, without doubt, the global benchmark for researchers on Triassic floras and, in my judgement, will remain so for many, many generations to come. The systematic approaches and interpretations (e.g. the ‘palaeodeme’) in the Monographs and their ‘individual’ style have sometimes proven controversial, generating interest and debate across a wide spectrum of the palaeobotanical community. This fact, together with the phylogenetic significance of many of the plant fossils, the high biodiversity with many new species, genera and higher taxa, the organic connection or association of sterile and fertile material, the quantitative documentation of plant fossil assemblages and the associated insect fossils, with trace fossils of insects feeding on plants, gives the series a very wide interdisciplinary relevance and significance.

I have awaited the fern volume with genuine personal interest as I have had a career-long passion for fossil ferns since first discovering Paleogene material of dispersed *Acrostichum* sporangia, *Azolla* megaspores and microspore massulae and pyrite permminer-alised rachides during my Ph.D. studies in the mid 1970s. I have not been disappointed. The fern volume possesses all of the best attributes of the previous volumes and further benefits from the addition of colour photographs. Although the authors express some reservation about the quality, I found the draft colour images to be excellent and to have particular value for conveying the preservation states and sedimentological context. The black-and-white photographs and annotated line figure sketches, the latter such a distinctive feature of the Molteno Monographs, are once again of high quality with excellent detail. I found myself easily spending extra time looking at each draft page of sketches because of the wealth of information that they convey.

The huge amount of care and effort that has gone into completion of the fern volume (as with others in the series) gives the Molteno Monographs a status of their own. Some 27 000 catalogued slabs from 100 assemblages have been examined with ferns being recovered from half of the assemblages. The fern fossils described include 18 species in seven genera with fertile material and a further 18 species in eight genera known only from sterile fronds. The authors recognise that some of the fertile material requires further study and, although currently included in the ferns, the affinity of three species is uncertain as sporangia are merely inferred. Many specimens of each species are used in the descriptions, sketches and photographs such that variation is truly well documented. Fertile fern material is ascribed to the Marattiaceae, Osmundaceae and Dipteridaceae with most being named as new species and with three new genera of Osmundaceae. One of these is of particular significance as the material comprises a more or less complete reconstructed plant based on a rooted horizon where *in situ* rhizomes occur with attached petioles and associated sterile and fertile fronds. It is considered similar in many ways to *Todea* growing in Africa today. About half of the genera of Molteno ferns also occur in the Triassic Nymboida flora from Australia, though they are considered to be distinct at specific level. The Molteno ferns volume is not only an extremely valuable contribution to current fern palaeobiology but it also provides the potential for much future research, especially for Triassic fern biogeography, for fern phylogenetic studies and for tracking palaeobiodiversity of key taxa through time (such as the Osmundaceae).

If my understanding is correct, this fern volume gets near to completing the series of Molteno Monographs. So I find myself asking—what will John and Heidi (and their respective partners and families) do with all their spare time when the last volume rolls off the press?! I sincerely hope that they will be able to continue with their palaeobotanical researches for as long as they themselves wish and I congratulate them for their work to date on the Molteno: a spectacular achievement of long-lasting scientific value.

Margaret E. Collinson
Professor of Plant Palaeobiology
Royal Holloway University of London
26 February 2007
My research into fossil plants was initiated by Dr Edna Plumstead during my B.Sc. (Hons) year at the University of the Witwatersrand, Johannesburg. Dr Plumstead was an enthusiastic palaeobotanist and an early proponent of the theory of Continental Drift. But it was Prof. Tom Harris who sparked my interest in fossil fertile ferns during my stay of three months (1968) at Reading University where I was studying the techniques of cuticle preparation. It was there that I experienced my first English spring with carpets of crocus and daffodils flowering on the campus grounds. Over the Easter Break, Prof. Harris and his wife took me to the north Yorkshire coast. Here we hiked beneath the towering sea cliffs and I made my first acquaintance with Jurassic plant fossils that were mainly exposed in fallen blocks on the beach. One day we became ‘swoon’ as Prof. Harris called it. Returning under the cliffs to Whitby we were caught by the rising tide and had to wade through ever deepening water. Harris dismissed it as a ‘small matter, we would soon be dry and warm again’. We plunged on and soon were climbing up to the ruined abbey above Whitby. And in the breeze it was not long before we were again dry and warm!

Prof. Harris was well known for his work in the 1930s on the East Greenland fossil floras and was now busy with Volume Four (Ginkgoales & Czekanowskiales) of the Yorkshire Jurassic Flora. He inspired me to describe the Molteno Triassic flora and that has become my lifetime’s work. Together with JMA we made a comprehensive collection of the Molteno flora over the following thirty years.

In the 1990s, while collecting further fern specimens for our work on our envisaged non-gymnosperm volume, JMA discovered Kammaskoppia, a unique fossil plant with fruit and leaves attached to a stem, and Fredlindia, an equally unique whorled bennettitopсид cone. These finds diverted us from our fern studies and instead resulted in our publication in 2003 of Heyday of the gymnosperms volume and of Brief history of the gymnosperms in press. Now, at last, we are planning the completion of the Molteno Monograph series.

In 2002 I took early retirement and moved with my partner, Keith Holmes to that other Gondwana continent, Australia. Keith is describing the rich biodiversity of the Middle Triassic Nymboida flora of eastern Australia. However, I will continue to spend some time back in South Africa each year till the Molteno project is completed.

I write this preface having just returned from the 7th European Palaeobotanical and Palynological Association Congress in Prague, the Czech Republic, where I presented the results of this study at the Fern Symposium held as part of the Congress. I trust that this volume will add to our understanding of the diverse nature of the evolution and systematics of ferns.

Heidi M. Anderson
Pretoria, 16 September 2006.

Between completing the pencil roughs of my half of the sketches for this volume and doing the inked finals, I shattered my right radius and wrist. I am obligately right-handed. It was late in May some five months back as the last of the autumn leaves were falling. The following two weeks had been dedicated to those pen sketches.

Doing science like doing art is inseparable from the scaffolding of one’s life. Be it the way our brains took in the world in our earliest few years, or the country in which we chance to find ourselves, or who were around at impressionable moments, or whether we break a limb at some inconvenient time, it all shapes our science. It is all there in our Molteno volumes; it is all there in this fern volume. That Heidi and I both grew up in South Africa as a consequence of Hitler’s war, that we should cross paths doing our B.Sc. Honours with modules in palaeobotany at the University of the Witwatersrand, that there were a host of splendid characters concentrated there at the time, and that the Molteno—with its unmatched biodiversity and almost endless potential—should occur at this distant end of Africa, are all a part of the tapestry that is life and science. One recalls Darwin’s reflection that he ended up on the five-year Beagle voyage (‘by far the most important event in my life’) as a consequence of the shape of his nose and that his uncle Josiah Wedgwood drove him thirty miles to Shrewsbury (‘which few uncles would have done’).

As I type this preface, my final contribution to our fern manuscript, I consider my wrist. I recollect telling the kindly orthopaedic before he chose ‘radical surgery’ (introducing a plate and screws) that my right hand ‘is my most important organ’ and that he must please get it working again. And so he did. At least I know I can still type and do pen sketches. Whether I will be able to wield a geology hammer with my customary vigour to quarry further into the Molteno remains to be seen.

John M. Anderson
Pretoria, 11 October 2006
A comprehensive description of the Filicophya (ferns) from the Late Triassic Molteno Fm., Karoo Basin, South Africa is made. This is based on an overall collection of over 27,000 catalogued slabs from 100 assemblages (taphocoenoses), 50 of which include ferns. These are placed conservatively in three orders and three named families, including 18 species in 7 genera of fertile ferns and 30 species in 15 genera of infertile material (of the latter, 18 species in 8 genera are known only from sterile fronds). The total filicophyte diversity, after consideration of likely and possible affiliations, is 34 species in 14 genera. A few of these may prove to be fern-like gymnosperms. Amongst the fertile ferns are the previously known genera *Drepanozamites* (1 species), *Asterotheca* (3 species), *Osmundopsis* (4 species) and *Dictyophyllum* (2 species); and the newly named genera *Rooitodites* (2 species), *Birtodites* (1 species) and *Elantodites* (5 species). The sterile ferns include the previously known genera *Drepanozamites* (1 species), *Parsorophyllum* (1 species), *Cladophlebis* (8 species), *Sphenopteris* (1 species), *Nymbopteron* (1 species), *Stormbergia* (2 species), *Dictyophyllum* (1 species), and *Nymboidiantum* (1 species); and the new genera *Displinites* (1 species) and *Molteniella* (1 species).

The material is almost invariably disarticulated. At only one locality, Kannaskop, has a complete fern (*Rooitodites integra*) comprising rhizomes, fronds and sporangia been found. This can be compared with the extant *Todea barbara* still growing in South Africa.

A census of the ferns thus far described from the Gondwana Triassic (Molteno included) amounts to a total of 40 genera with 124 species. The most diverse fern flora, with 23 genera and 46 species, is from the well-sampled and recently revised Middle Triassic Nymboida Coal Measures of New South Wales, Australia.

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**DEDICATION**

We dedicate this volume to our four parents, Rolf and Rösli (Schwyzer), Gordon and Dora (Anderson), who fashioned us in one way or another towards having made this Molteno collection and to writing it all up. We find it poignantly symbolic that the last three of the quartet, Rösli, a great lover of neoclassical music, passed away (June 2006) in the year of Mozart’s 250th anniversary. All reached their late eighties or early nineties. From them we learned in our own ways to love the natural world, and to discover that our world was far greater than the present time and place. It is they who steered us to and through university and hence into some insight into bygone eras well before the appearance of the hominids and ultimately of *Homo sapiens*. 
ACKNOWLEDGEMENTS

As for our previous Molteno volumes, there are numerous persons in widely ranging walks of life that have made this work possible. First are the many farmers on whose land the localities occur and whose hospitality and help with excavations has made this life-long undertaking so much more rewarding. Of these, the Tennant and Terblanche families deserve particular mention. On their farms, one low in the Molteno sequence and the other in its highest levels, occur two of the four richest of our Molteno localities. From each we have collected over 2 000 catalogued slabs and spent over 500 man-hours cleaving fossiliferous blocks (on site or later in the lab).

In this volume we have shifted from our more usual practice of naming new taxa (of which there are numerous in the Molteno) after localities or diagnostic morphological features, to commemorating friends, family and colleagues. Either in accompanying us on collecting trips or helping back in the city, they have clearly assisted in furthering our research. These include: James Kitching and Brian Turner from our earlier days at the Bernard Price Institute for Palaeontology, University of the Witwatersrand; Bernard de Winter and Donald Killick of the Botanical Research Institute (now SANBI); Rösli and Rolf Schwyzer, Heidi’s parents; Felix, Evie, Rosemarie and Barbara, Heidi’s siblings; Anna Katharina Benecke, Janet Fatti, and Katherine Ambrose, palaeobotanical colleagues and friends; Joy, Den, Stuart and Alison Tennent, and Fred and Linda Terblanche of the farming districts Bird’s River and Aasvoëlberg, respectively.

We owe special thanks to Keith Holmes (palaeobotanist and husband of HMA) and to Marijke Marchal (teacher and wife of JMA). Each has played a very close role in our research on the Molteno in general and on this fern volume in particular. Keith has added considerably through having recently completed writing up his own work on the Nymboida flora, richest of all known Gondwana Triassic fern ‘formations’, and in direct assistance in typing and proofreading. Marijke accompanied JMA on several field trips dedicated specifically to filling out the collections from fern-rich localities.

Continuing support from SANBI is gratefully acknowledged. In the production of this volume, we wish to thank especially Louisa Liebenberg (leader of the publication team), Elizma Fouché (typesetting and layout), Gerrit Germishuizen (technical editing), Sandra Turck for the cover design and Gill Condy for the watercolour renderings on the cover. Natasha Mothapo and Tebogo Mashua, scientific officers for Gondwana Alive, have each put in a good deal of time on the manuscript—from the sizing of colour photographs to the typing of captions. Typing of tables was done by Sello Matseke and Linda Shaba. Adela Romanowski (now retired and living in New Zealand) processed the black and white photographs, a skill now increasingly difficult to find. Lambert Smith took all the digital colour photos and guided them through the printing process. His devotion to his art and to quality control throughout has been deeply appreciated.

SPONSORSHIP

We wish to express our gratitude to Fred and Linda Daniel for sponsoring the colour plates appearing in this volume—for enabling us to break into this new territory in our series of Molteno volumes. There is something rather potently coincidental in their generosity. Fred and Linda are deeply devoted to building their ‘Nkomazi Wilderness’ (on the Komati River), an extensive tract of prime country in the Barberton Mountains of Mpumalanga in the northeastern part of South Africa. Fred refers to the reserve as the ‘Cradle of Life’ which has a ring of deep reality about it—the Barberton Greenstone Belt dates to 3 570–3 060 million years ago and represents the largest and best preserved stretch of the world’s oldest known landscape. In these strata are preserved the world’s oldest known fossil bacteria (at 3 472 Ma).

The word Nkomazi in the local Swazi tongue means ‘place of the female cow’, or more figuratively, ‘mother, nurturing’—a fitting name for this wilderness being restored in the interest of nurturing the soul of future generations.

The word (uMkhomazi) in the local Zulu tongue means ‘the place of the cow whales’. A large number of whales once used the estuary of the Umkomaas River as a nursery, giving birth in the shallows. The Zulus named the river after this spectacle.

Nkomazi and Umkomaas, place of origin and place of peak diversity respectively, places of nurturing!
MOLTENO FERN BIODIVERSITY & RELATED TOPICS
MOLTENO FERN BIODIVERSITY & RELATED TOPICS

1. INTRODUCTION

This monograph on the Molteno ferns is the fourth in a series describing the Late Triassic Molteno fossil flora. The first volume (And. & And. 1983) dealt with Dicroidium, the most important genus in the flora. A photographic overview of the flora was also presented, with the ferns being illustrated on plates 3–9. Subsequent books dealt with the gymnosperm foliage (And. & And. 1989) and gymnosperm fructifications (And. & And. 2003). Regular reference is made here to these earlier works and where general information or methodology has already been published it is not repeated.

The Filicopsida evolved (Andrews et al. 1970; Stewart & Rothwell 1993; Taylor & Taylor 1993) in the Devonian and by the Carboniferous had greatly diversified, with some growing into large tree ferns. By Triassic times and in the Molteno flora, the ferns were still diverse and widespread but formed a smaller component of a flora that was dominated by the gymnosperms. In the present world the position is similar except that angiosperms now dominate. Many extant ferns may be regarded as ‘living fossils’ with their origins tracing back to the Cretaceous or earlier.

The Filicopsida are known from all early Mesozoic floras and have been described comprehensively for the Rheo-Liassic flora of Greenland (Harris 1931, 1932) and the Jurassic flora of Yorkshire (Harris 1961). Dobruskina (1994) gave a general review for the Triassic of Eurasia. The Late Triassic floras of North America, including the ferns, have been reviewed by Ash (1969, 1999), Ash & al. (1982) and by Ash in Anderson et al. (2007). Gondwana Triassic fern fronds were first described by Morris (1845). Notable recent references for the southern floras include the fern flora from Nymboida, New South Wales (Holmes 2001, 2003), including a marattiacese fern (Webb 2001); an osmundaceous whole-fern plant (Phipps et al. 1998) and permineralised sporangia (Phipps et al. 2000) from the Lashly Fm., Transantarctic Mountains, Antarctica; a new species of Gleichenites (Herbst 1996) and a fern flora (Herbst et al. 1998) from La Ternera Fm., Copiapo, Chile. Tidwell & Ash (1994) gave a good global overview of selected Triassic to Cretaceous ferns. Anderson et al. (1999a) provided a general review of plant colonisation and diversification (including ferns) for Gondwana.

The palaeoecology of ferns is gaining interest as witnessed by a symposium held in 2000 on ‘The Ecology of Ferns Through Time’ (Collinson & Van Konijnenburg-van Cittert 2002). The Triassic ferns from Laurasia were reviewed by Van Konijnenburg-van Cittert (2002), but no equivalent exists for Gondwana occurrences. Cantrill (1998) gave an excellent description of Lophosoria from the Cretaceous of Antarctica and, by comparison with living material, gave an interpretation of Cretaceous climatic conditions.

In the Molteno, Filicopsida occur in each of the seven primary habitats of the Floodplain Biome (published in colour in Anderson et al. 1999b). Each supported a distinctive plant/insect co-association. The Fern/Kannaskoppia meadow is the only habitat dominated by ferns; it formed low-diversity herbaceous assemblages that occupied the sand bars of the braided river system. A good example of this habitat occurs at Kannaskop (Kan 111 Ast sp/A) where a root horizon is preserved containing fern rhizomes with attached petioles and associated fronds. This is the only case in the Molteno flora where a complete fern bearing both fertile and sterile fronds has been found in the position of growth.

This review of the Molteno ferns allows comparisons to be made with other well-documented Gondwana Triassic floras. The Nymboida flora from the Basin Creek Fm. (Ladinian) in Australia (Holmes 2001, 2003) has revealed a remarkably diverse fern assemblage with a total of 23 genera and 46 species. Nine genera (4 fertile and 5 sterile) from this Nymboida flora occur also in the Molteno, but the species are generally distinct. After Nymboida, the Molteno yields the second most diverse fern flora known for the Gondwana Triassic. Other southern Triassic floras require further collecting and revision to enable meaningful comparisons to be made with those of the Nymboida and Molteno.  

2. SAMPLING

Molteno ferns have been described by Feistmantel (1889), Seward (1908, 1911), Du Toit (1927) and others. Our collecting commenced in 1968, with the most intensive periods being in the early 1970s and early 1980s.

For sampling strategies, methods and approach see And. & And. (1983, pp 2–29; 1989, pp 5–17; 2003, pp 2–11). A table and map of the ‘localities’ and the 100 assemblages (taphocoenos = TCs) are given in And. & And. (1989, p. 29) and And. & And. (2003, pp 8, 9).

Our own extensive collections—belonging to the South African National Biodiversity Institute, Pretoria, (PRE/F/-) and the Bernard Price Institute, Johannesburg (BP/2/-)—provide the basis for the data included in this publication.

3. FREQUENCY & ABUNDANCE

Ferns occur in 50 of the 100 Molteno taphocoenos (TCs) covered in this study (see Tab. 6) and fall in five abundance classes (see And. & And. 2003, Tab. 8, p. 13, for definitions): a) co-dominant (20–69%): at 7 TCs (63% Kan 111; 52% Kon 211/221; 40% Tln 131; 20% Pen 221, Aas 111 & Cal 211); b) abundant (6–19%): at 1 TC (9% Ask 111); c) common (3–5%): at 5 TCs (5% Dor 111 & Pen 321; 4% Kna 111 & Ela 112; 3% Pen 411); d) sparse (1–2%): at 5 TCs (2% Boe 111; 1% Kom 111, Kon 223, Kon 222 & Umk 111); e) rare to extremely rare (below 1%): at the remaining 32 TCs which yield ferns.

In Tab. 6 (TCs/species matrix) the abundance and frequency of the Molteno ferns is documented. Where the abundance of fern fronds in an assemblage is 1% or greater, it is included as a percentage of the flora (given as a bold number on the table). Where they are rare (below 1%) the number of individuals is recorded (given as a mild number).

4. AFFILIATED ORGANS

In the Molteno collections, only a few specimens have associated fertile and sterile pinnules on the same frond (e.g. Rootitoides pulchra). A notable occurrence is that of R. integrata at Kan 111 for which it has been possible to reassemble the whole plant based on in situ rhizomes and associated fertile and sterile fronds. However, at most localities, individual parts are separate but where possible we have affiliated fertile and sterile fronds. The results are shown on Tab. 2. For our usage of affiliation criteria and reliability grades (from 1: marginal to 5: certain) see And. & And. (1985, p. 85; 2003, p. 16).

Whole fern plants are known, though extremely rarely, from the Gondwana Triassic. Phipps et al. (1998) described Osmunda claytoniites from the Allan Hills, Antarctica, based on a good rhizome with petioles and two croziers attached and associated with fertile and sterile fronds. Holmes (2001)
described *Herbstopteris colliveri* and *Osmundopsis scalaris* from the Nymboida Coal Measures of eastern Australia based on radiating fronds and associated rhizomes.

From the Laurasian Triassic are further examples. Schweitzer (1978) described some excellent material of *Todites princeps* from the Raheo-Liassic of Iran with attached roots, rhizomes and fronds. He was able to show how it propagated vegetatively and produced young plants. From North Carolina, USA, the plant *Pekiopites auriculata* has been reconstructed based on sterile fronds attached to rhizomes (Delevoryas & Hope 1978). Ash et al. (1982) reconstructed the *Phlebopteris smithii* plant from the Late Triassic Chinle flora, western USA, based on whole leaves from numerous localities. *Anomopteris mougeotii* (Grauvogel-Stamm & Grauvogel 1980), very common in the early Middle Triassic Voltzia Sandstone of France, is known from sterile and fertile fronds and as whole juvenile plants. It is characterised by large aphlebia at the base of the fronds and by sporangia with a ring of thickened cells at the apex.

5. MEASURING BIODIVERSITY

Molteno Fm.

Previous estimates of Filicophyta diversity in the Molteno (And. & And. 2003, p. 31) are revised in this study to 3 orders, 3 families, 16 genera and 37 species (Tabs 1, 4). As more fertile fern material becomes available the number of families in particular will increase. At present only 7 genera and 18 species are based on fertile material, with much sterile material remaining unaffiliated (Tab. 2).

With further details on the structure of the assumed sporangia as described for *Asterotheca killickii*, *Osmundopsis petiolaris* and *O. racemosus* becoming available, these species may in the future prove to be gymnosperms and not ferns.

Gondwana Triassic (GT)

A total of 40 genera and 124 species of ferns have been described from Gondwana Triassic (GT) strata (Tab. 4). Of these, 23 genera and 72 species (3 orders, 6 families) are based on fertile material. This represents, no doubt, far from a comprehensive picture for this opening period of the Mesozoic for the southern supercontinent: the African contribution is based almost exclusively on the collections from a single formation (the Molteno); Antarctica and India, with just three and five species respectively, are clearly hugely under-represented; well over half of the Australian taxa (18 genera with 35 species of a total 25 genera with 60 species) have been described as new by Holmes (2001, 2003) in two recent papers on the Middle Triassic Nymboida flora based on just two well-sampled localities; the South American tally of 14 genera with 38 species is the unrevised accumulated result of many authors over a century or more from many widely scattered formations.

Thorough sampling and description of the fern content from the most productive formations through the Triassic across Gondwana awaits the next generation of paleobotanists. A Gondwana-wide revision of the group would then be on the cards. Nevertheless, a sense of the fern diversity in the wake of the end-Permian extinction is at hand. When considered that very few taxa—just 7 species—are currently recognised from more than one of the Gondwana Triassic continents, the final diversity total might be expected to rise considerably.

6. PROMINENCE (COLONISATION SUCCESS)

The terms prominence and success are applied in our work synonymously. The prominence of a genus in the Gondwana Triassic Empire refers to its relative importance or consequence and is measured as the sum of the five attributes—Frequency, Ubiquity, Diversity, Abundance and Longevity (FUDAL). For a definition of these terms refer to And. & And. (1989, p. 36; 2003, p. 26). See Tab. 10 a,b, ‘Molteno ferns: prominence in Gondwana context’.

All illustrated fern literature pertaining to the Gondwana Triassic has been considered (see hypodigm charts, Tab. 11) while literature of other regions and periods is referred to only when relevant. Our current determinations/identifications of taxa in previous Gondwana Triassic publications appear in the final column of the hypodigm charts (Tab. 11).

7. MOLTENO BIOME & HABITATS

The Molteno Biome was first described in Cairncross et al. (1995). The vertebrate and insect occurrences were discussed subsequently in Anderson et al. (1998). The distribution of the fruits and structures in the seven Molteno habitats was provided in And. & And. (2003, pp 30–39). Ferns occur in all seven primary Molteno habitats and, where feasible, the preferred habitat and habit of each genus is indicated on the genus page.

8. FORMAT OF SYSTEMATICS SECTION

a) Introduction

The layout of the genera and species pages (including pen sketches and black-and-white plates) follows that of And. & And. (1989, pp 22–25) and And. & And. (2003, pp 42–45) with the addition of the heading ‘Rarity and quality of the fertile Molteno material’. The treatment of fertile taxa appears first and is followed by that of taxa known only from sterile material. For definitions of reconstruction grades used for the drawings (R1, no intended reconstruction; R5, extensive reconstruction), see And. & And. (1989, p 22) and And. & And. (2003, p. 44).

b) Rarity and quality of the fertile Molteno material (Tabs 6–9)

As with the gymnospermous taxa of the Molteno—where 9 of 20 ovulate genera and 4 of 15 microsporangiate genera (And. & And. 2003, Tabs 9 a,b, p. 13) are each known from just one of 100 sampled TCs, so the fertile ferns of the Molteno are particularly rare. This holds in regard both to frequency and abundance. Of the 18 fertile fern species, 8 are known only from the reference palaeodeme, and a further 7 occur in only 2 or 3 palaeodemes. In abundance, the fertile material (within the reference palaeodemes) ranges from ‘rare’ to ‘extremely rare’ verging on ‘vanishingly rare’.

Again as for the Molteno gymnosperms (And. & And. 2003), this marked infrequency and rarity of the fertile fern material, in spite of the extensive (100 TCs) and intensive (27 000 catalogued slabs) collecting overall, points to the ‘preserved’ fern diversity in the formation far exceeding the ‘observed’ diversity (Anderson et al. 1996).

c) Colour plates (Tab. 8, pls 101–152)

After completion of the original manuscript of the Molteno ferns, the opportunity arose to prepare a comprehensive set of digital colour-plates of the best-preserved fertile material. Associated with this has been the chance to make a closer study of the comparative morphology of the sporangia at palaeodeme, species and generic levels and to assess the implications concerning fern diversity in the Late Triassic.

In completing our series of monographs on the Molteno flora, we have found ourselves at a difficult interface where the black-and-white photography of the past is being progressively displaced by colour photography. Simultaneously, the threshold between traditional colour photography and digital-colour photography is being crossed. It is generally anticipated that digital-colour will be ubiquitously used within just a few years.
As the gap in cost between the printing of black-and-white and colour rapidly narrows, so the appearance of colour in scientific publications is simultaneously growing. This is particularly the case in palaeobotanical (or palaeoentomological) works. There can be little doubt that colour adds an extra dimension to the presentation of our fossil material. The contrast between different deposits (TCs), between specimen and sediment, and between morphological details within any particular specimen, is clearly enhanced with the full spectrum of colour at hand.

This exercise has not been without its problems. Currently available technology for capturing close-up images of fern sporangia ranging in size from 0.2 to 0.5 mm, for instance, seems not to be readily equal to the task. The optimal interplay between microscope, camera and computer software seems not yet to have been perfected. Reflected-light microscopy has inherent problems not experienced in transmitted-light microscopy. Scanning-electron microscopy appears, yet to have been perfected. Reflected-light microscope photography has inherent problems not experienced in transmitted-light microscopy. Scanning-electron microscopy appears, likewise, not yet able to adequately fill the gap: the technology lags behind our present needs.

9. FERN CUTICLES

A preliminary analysis of Molteno fern cuticles has not yielded much useful morphological data for classification. The Molteno localities with potential cuticle are discussed in And. & And. (1989, p. 56). Cuticles were macerated from Lit 111 (the genus *Nymboidiantum* yielded some structure based on 12 samples) and Umk 111 (the genus *Cladopylepis* yielded no structure based on 18 samples). On occasional fronds, cellular structure (presumably epidermal) is visible at high magnification. This is present at Umk 111 and also at localities not yielding carbonaceous cuticles, e.g. Gre 121. Further examples are listed under *C. paucinervia* and *C. roseomariae*. Similarly, some sporangial structure is preserved, e.g. at Ela 112, of *Elatodontes turneri*. Opportunity exists for further research on Molteno fern microscopic structure utilising the Jeol Scanning Microscope (And. & And. 2003) and for updating the initial study of spores (And. & And. 1983, pp 28, 29).

10. CLASSIFICATION OF MOLTENO FERNS

A classified list of the Molteno ferns is provided in Tab. 1 and a classified pictogram key in Tab. 5. Sterile fronds with unknown fertile affiliations are classified separately under the most probable order (prefix by ‘? ’). When knowledge of these ferns increases through the discovery of fertile fronds they may be more confidently classified. Two general classifications are given in Tab. 3 a, b for comparison: the first by Meyen (1987) covers all the fossil groups; the second for extant ferns is by Woodland (2000). The classified list of Gondwana Triassic ferns follows in Tab. 4 and is based on our identifications of all the illustrated Gondwana Triassic ferns which are listed on the hypodigm charts (Tab. 11).

The present lack of consensus on the higher classification of true ferns was discussed from a fossil perspective by Stewart & Rothwell (1993) and Taylor & Taylor (1993). Kramer (1990), for instance, resolved the dilemma of which classification to follow for extant ferns by creating his own classification, as published in Volume I of ‘The families and genera of vascular plants’ edited by Kubitzki (1990).

Rothwell (1999) addressed the question of global fern phylogeny by applying numerical cladistic analysis of morphological characters in both extinct and living taxa. His results placed the ferns and allied groups in a polyphyletic group that resolved into three clades. Clade 3 encompassed all extant fern families including the Marattiaceae and Ophioglossales. Furthermore, he concluded that relationships among the filicolean families are not adequately resolved. A phylogenetic study of extant ferns, based on plastid and nuclear genomes, with a special focus on the early divergences among leptosporangiate lineages was undertaken by Pryer et al. (2004).

Of particular interest to our Molteno fern study is that Rothwell (1999) included the extant genus *Osmunda* in the ‘Basal’ living Filicales, while Pryer et al. (2004) confirmed that the Osmundaceae are a sister group to the rest of the leptosporangiates. The three extant genera in the family Osmundaceae are of very low diversity. In the Mesozoic, ferns allied to *Osmunda* were dominant from probably the Early Triassic but certainly by the Late Triassic to the Early Cretaceous (Tidwell & Ash 1994). Schneider et al. (2004) reported that ‘polypod ferns’ diversified in the Cretaceous, possibly at the same time or after the diversification of angiosperms and today account for more than 80% of all living fern species. The most common ferns in the Molteno fall in the Osmundaceae. Many fern taxonomists tend to include the Osmundaceae with other fern families having sporangia with a distinct annulus and that are often arranged in sori. However, Meyen (1987), taking into account the fossil record, recognised the Osmundales as a distinct order (Tab. 3a). A recent global classification by Woodland (2000) also recognises this distinction (Tab. 3b). This separation is useful in classifying the Molteno ferns. We use the following three orders:

**Order Marattiaceae**: Ferns with sporangia having a multi-layered wall and grouped in synangia.

Recorded from the Carboniferous and Permian (Stewart & Rothwell 1993) and represented by the extant genera *Angiopteris*, *Christensenia*, *Danaea* and *Marattia* (Kubitzki 1990). In the Molteno, the order includes *Drepanozamites* (the first Gondwana record of this genus that was first described from the Rhaetic of Greenland) with two new species and *Asterotheca* represented by 3 species.

**Order Osmundaceae**: Ferns with sporangia having a multi-layered wall and a group of thickened cells but without a distinct annulus; sporangia not arranged in sori.

Known from the Upper Permian (*Palaeosmunda*, Gould 1970) or possibly even earlier (Tidwell & Ash 1994; Skog 2001) and represented by the extant genera *Todea*, *Osmunda* and *Leptopteris*. In the Molteno the order is very well represented by 4 species of *Osmundopsis* and a further 3 new genera including 8 new species.

**Order Polypodiales**: Ferns having homosporous sporangia with a single-layered wall and a distinct annulus; sporangia usually occurring in sori.

They are known possibly from the Palaeozoic with good records of extant families from the Jurassic (Taylor & Taylor 1993, p. 437). This order is represented in the Molteno by 3 species of *Dictyophyllum* in the family Dipteridaceae. *Dictyophyllum* reached its zenith in the Late Triassic–Early Jurassic and waned towards the end of the Jurassic. Today the family is represented by the single genus *Dipteris*. 

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**Introduction**
Tab. 1. Molteno ferns (Filicophyta): classified list

Genera & species: listed in order of appearance in this volume.
Fertile & infertile genera: separated by broken line.
Diversity: 3 orders, 3 families, 16 genera, 37 species (total);
3 orders, 3 families, 7 genera, 18 species (fertile).

Fern crozier, incertae sedis

The only fern crozier found in the Molteno is illustrated here (Fig.1). Other circinate fronds from the Gondwana Triassic have been reported: by Phipps et al. (1998, fig. 5), two croziers attached to a rhizome from Antarctica; and by Holmes (2003, fig. 34D), a single specimen from the Nymboida flora of Australia that is closely similar to the Molteno specimen.
### DIVISION CLASS ORDER FAMILY

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<th>Detached sterile foliage (SP)</th>
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Fertile: 7 genera, 18 species
Sterile: 15 genera, 30 species
8 genera, 18 species only known as sterile

Total filicopsid diversity (after merging likely & possible affiliates): 14 genera, 34 species

**Tab. 2. Molteno ferns: affiliated foliage**

*Fertile foliage/sterile foliage attached:* in seven cases.

*Fertile foliage/sterile foliage affiliates established:* in seven cases.

*Affiliation reliability grades:* numbers indicate grades 1–5 (And. & And. 2003, p. 16).

Grade 1, marginal—marginal likelihood of affiliation;
Grade 2, poor—most feasible affiliation;
Grade 3, fair—probable affiliation;
Grade 4, good—virtually exclusive likelihood of affiliation;
Grade 5, certain—organic attachment.

**RP:** Reference Palaeodeme.

**SP:** Sister Palaeodeme.
### Table 3a
**Global classification: fossil & extant ferns**
from Meyen (1987)

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### Table 3b
**Global classification & diversity: extant ferns**
adapted from Woodland (2000)

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**Total**: 37 families, 260–318 genera, 10 934–11 101 species

**Note**: the above orders are Woodland’s subclasses

---

**Tab. 3a, b. Global classification of ferns**

*Supra-generic classification*: consensus for ferns is far from reached as yet.

*Comparative classifications*: we select for comparison two of the many very variable published classifications for reference, the first to include both fossil & extant ferns, the second covering extant ferns and their diversity.
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**Classification**

**Division:** Rhyniopsida, Marattiales

**Family:** Marattiales

**Genus & species:**
- *Drepanozamites dubitii* sp. nov. (Ha 213)
- *Marattia sp. Playford et al. 1982*
- *Ogmos adinus* Webb 1983
- *(Danaeopsis) recunda* Herbst 1988
- *Rhynipteris walkowii* Holmes 2001
- *Scolecopteris antarctica*

**Family:** Asterothecaeeae

**Genus & species:**
- *Gleichenites cachivaritensis*
- *Gleichenipteris antarcticus*
- *Herbstopteris colliveri*
- *Scolecopteris antarctica*
- *Rhinipteris walkowii*
- *Marattiopsis sp. Playford et al. 1982*
- *Mesopteris australis* Playford et al. 1982
- *Ogmos adinus* Webb 1983
- *(Danaeopsis) recunda* Herbst 1988
- *Rhynipteris walkowii* Holmes 2001
- *Scolecopteris antarctica*

**Family:** Asterothecaeeae

**Genus & species:**
- *Gleichenites cachivaritensis*
- *Gleichenipteris antarcticus*
- *Herbstopteris colliveri*
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**Family:** Asterothecaeeae

**Genus & species:**
- *Gleichenites cachivaritensis*
- *Gleichenipteris antarcticus*
- *Herbstopteris colliveri*
- *Ogmos adinus* Webb 1983
- *(Danaeopsis) recunda* Herbst 1988
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**Family:** Asterothecaeeae

**Genus & species:**
- *Gleichenites cachivaritensis*
- *Gleichenipteris antarcticus*
- *Herbstopteris colliveri*
- *Ogmos adinus* Webb 1983
- *(Danaeopsis) recunda* Herbst 1988
- *Rhynipteris walkowii* Holmes 2001
- *Scolecopteris antarctica*
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</table>

Tab. 4. Gondwana Triassic ferns: classiﬁcation & occurrence

**Fertile genera:** included ﬁrst in the table (to broken line).
**Infertile genera:** included second in the table (following broken line).
**Genera & species:** included for convenience alphabetically within families (sequence thus differs from Molteno classiﬁcation).
**Source of data** (non Molteno): Hypodigm table (Tab. 11) in this volume.
**Diversity:** unidentified species (e.g. *Asterotheca* spp) are, for convenience, counted as single species in diversity tallies.
Tab. 5a, b. Molteno ferns: genus & species panorama, with morphological terminology (pp 10–15)

**Panorama:** pen sketches of all 16 genera & 37 species of Molteno ferns are covered (from one to several sketches of each species).

**Morphological terminology:** the panorama also functions as a key to the fern terminology used.

**Molteno monographs:** for examples of similar coverage for Molteno gymnosperms, see And. & And. 1989, pp 70–73 (panorama of Dicroidium & affiliated strobili) & And. & And. 2003, pp 50–53 (morphological terminology of female & male strobili, Pinopsida to Bennettitopsida).

### Table 5a Molteno ferns, fertile taxa (pp 10–13)

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<td>* Asterotheca chevronervia Holmes 2001 (Kon 223) f s</td>
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<td></td>
<td>* hamata sp. nov. (Umk 111) - s</td>
<td>* dewinteri sp. nov. (Hla 213) f s</td>
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<td>* killickii sp. nov. (Umk 111) f -</td>
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<td>Osmundales (fertile)</td>
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<td>Osmundopsis botryoides sp. nov. (Pen 311) f -</td>
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<td>* cf. O. scalaris Holmes 2001 (Kon 211) f -</td>
<td>* petiolaris sp. nov. (Umk 111) f -</td>
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<td>* racemosus sp. nov. (Aas 411) f -</td>
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<td>Rooitodites pulchra gen. et sp. nov. (Kon 211/221) f s</td>
<td>* interna gen. et sp. nov. (Kon 112) f s</td>
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<td>* Brintodites holmesii gen. et sp. nov. (Br 111) f s</td>
<td>Elantodites turneri gen. et sp. nov. (Ela 112) f s</td>
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<tr>
<td></td>
<td>* stuartii gen. et sp. nov. (Br 111) f s</td>
<td>* alstoniae gen. et sp. nov. (Br 111) f s</td>
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<td></td>
<td>* kilichnii gen. et sp. nov. (Kon 211/221) f -</td>
<td>* joydeniorum gen. et sp. nov. (Br 111) f s</td>
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<tr>
<td>Polypondiales (fertile)</td>
<td>Dipteridaceae</td>
<td>D. dutoiti (1, 2) (3, 4) (Hla 213) x s</td>
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<td>* Dicryptophyllum ellenbergii Fabre &amp; Greber 1960 (Mor 111) f s</td>
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<td>* bremenense Shirley 1898 (Tel 111) f s</td>
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<td>* shirleyi (Herbst 1979) Webb 1982 (Aas 411) - s</td>
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### Drepanozamites

- D. dutoiti (1, 2) (Hla 213) x 5
- D. harrisi (3, 4) (Umk 111) x 5

### Asterotheca

- A. chevronervia (Kon 223) x 5
- A. dewinteri (Hla 213) x 5
- A. killickii (Umk 111) x 5

**Morphological panorama**
Morphological panorama
Morphological panorama
**Morphological panorama**

**Elantodites**

1. Frond, tripinnatifid
   - x 1

2. x 2.5

3. x 5

4. Sporangium, lateral view
   - x 100

5. Annulus rays
   - x 100

6. Fertile pinna
   - x 2

7. Fertile pinnule
   - x 5

8. Sporangia
   - x 100

9. Fertile pinnule (sporangia partly shown)
   - x 0.5

10. Fertile pinnule
    - x 5

11. Sporangium
    - x 100

12. Frond bipinnate
    - x 1

13. Fertile pinnules
    - x 5

14. Sporangia
    - x 100

15. Sterile pinnule
    - x 1

**E. turneri** (1–5)
- All Ela 112

**E. stuartii** (6–8)
- All Bir 111

**E. alisoniae** (9–11)
- All Bir 111

**E. kitchingii** (12–14)
- Ela 112 (13, 14)

**E. joydeniorum** (15)
- Bir 111
### Table 5b Molteno ferns, sterile taxa (pp 14, 15)

<table>
<thead>
<tr>
<th>? OSMUNDALES (infertile)</th>
<th>Cladophlebis</th>
<th>C. rosemariae</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cladophlebis paucinerva Holmes 2003 (Umk 111)</td>
<td>- s</td>
<td>- s</td>
</tr>
<tr>
<td>&quot; rosemariae sp. nov. (Pen 321)</td>
<td>- s</td>
<td></td>
</tr>
<tr>
<td>&quot; katherineae sp. nov. (Umk 111)</td>
<td>- s</td>
<td></td>
</tr>
<tr>
<td>&quot; mollenensis sp. nov. (Umk 111)</td>
<td>- s</td>
<td></td>
</tr>
<tr>
<td>&quot; barbara sp. nov. (Umk 111)</td>
<td>- s</td>
<td></td>
</tr>
<tr>
<td>&quot; janetae sp. nov. (Aas 111)</td>
<td>- s</td>
<td></td>
</tr>
<tr>
<td>&quot; felixii sp. nov. (Umk 111)</td>
<td>- s</td>
<td></td>
</tr>
<tr>
<td>&quot; evelynae sp. nov. (Boe 111)</td>
<td>- s</td>
<td></td>
</tr>
<tr>
<td>Sphenopteris annakatiae sp. nov. (Kon 211/221)</td>
<td>- s</td>
<td></td>
</tr>
<tr>
<td>Birmoltia intervenatus gen. et sp. nov. (Bir 111)</td>
<td>- s</td>
<td></td>
</tr>
<tr>
<td>Nymbopteron ephippiata sp. nov. (Umk 111)</td>
<td>- s</td>
<td></td>
</tr>
<tr>
<td>Parsorophyllum africana Seward 1911 (Kon 211)</td>
<td>- s</td>
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</tr>
<tr>
<td>Stormbergia gardneri sp. nov. (Cyp 111)</td>
<td>- s</td>
<td></td>
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<tr>
<td>&quot; rosliae sp. nov. (Umk 111)</td>
<td>- s</td>
<td></td>
</tr>
<tr>
<td>? POLYPODIALES (infertile)</td>
<td>Nymboidiantum schwyzeri sp. nov. (Lit 111)</td>
<td>- s</td>
</tr>
<tr>
<td>Displinites variabilis gen. et sp. nov. (Umk 111)</td>
<td>- s</td>
<td></td>
</tr>
<tr>
<td>Molteniella terblanchiorum gen. et sp. nov. (Aas 411)</td>
<td>- s</td>
<td></td>
</tr>
</tbody>
</table>

**Total:** 16 genera, 37 species.

---

**Morphological panorama**

- **Cladophlebis**
  - **1.** C. paucinerva
  - **2.** C. rosemariae
  - **3.** C. katherineae
  - **4.** C. moltenensis
  - **5.** C. barbara
  - **6.** C. janetae
  - **7.** C. felixii
  - **8.** C. evelynae

- **Sphenopteris annakatiae** (9, 10)
  - **9.** Kon 211/221
  - **10.** frond tripinnate, pinnae opposite

- **Birmoltia intervenatus** (11, 12)
  - **11.** Bir 111
  - **12.** pinnule, venation twice-forked

---

**Legend:**
- x 1
- x 2.5
- x 0.5
Morphological panorama
<table>
<thead>
<tr>
<th>BARBESBERG</th>
<th>INDWE (G)</th>
<th>MAVAPUTI</th>
<th>QIRA</th>
<th>TSOMO</th>
<th>L</th>
<th>Molteno membrans</th>
<th>Molteno cycles</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
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<td></td>
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</tbody>
</table>

Note: The table contains data for various plant species and their characteristics.
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<thead>
<tr>
<th>Mafikeng</th>
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<th>Lebowa</th>
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<tr>
<td>1. D. assemblages</td>
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<td>3. D. altivulsi</td>
<td>s</td>
<td>s</td>
<td>s</td>
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<tr>
<td>gen.</td>
<td>s</td>
<td>s</td>
<td>s</td>
</tr>
<tr>
<td>spp</td>
<td>s</td>
<td>s</td>
<td>s</td>
</tr>
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<td>1. C. parvithorax</td>
<td>s</td>
<td>s</td>
<td>s</td>
</tr>
<tr>
<td>2. C. roseum</td>
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<td>s</td>
<td>s</td>
</tr>
<tr>
<td>3. C. latiforinae</td>
<td>s</td>
<td>s</td>
<td>s</td>
</tr>
<tr>
<td>4. C. moerens</td>
<td>s</td>
<td>s</td>
<td>s</td>
</tr>
<tr>
<td>5. C. barbara</td>
<td>s</td>
<td>s</td>
<td>s</td>
</tr>
<tr>
<td>6. C. jamato</td>
<td>s</td>
<td>s</td>
<td>s</td>
</tr>
<tr>
<td>7. Cladophlebus africana</td>
<td>s</td>
<td>s</td>
<td>s</td>
</tr>
<tr>
<td>8. S. rosliae (Umk 111)</td>
<td>s</td>
<td>s</td>
<td>s</td>
</tr>
<tr>
<td>9. S. variabilis</td>
<td>s</td>
<td>s</td>
<td>s</td>
</tr>
<tr>
<td>10. S. melale</td>
<td>s</td>
<td>s</td>
<td>s</td>
</tr>
<tr>
<td>11. S. rosliae</td>
<td>s</td>
<td>s</td>
<td>s</td>
</tr>
<tr>
<td>Matrix tables</td>
<td>s</td>
<td>s</td>
<td>s</td>
</tr>
</tbody>
</table>
Tab. 7. Molteno ferns: fertile material in the collection

**Taphocoenoses (TCs):** the 23 TCs yielding fertile ferns are arranged in stratigraphic sequence, youngest above.

**Taxa:** the 7 genera & 18 species of fertile ferns are arranged in classified sequence.

**Matrix:** figures indicate abundance in the Molteno collection.

**Abundance:** bold = % estimate made at site;
mild = individuals in curated collection (where <1%).

*Dictyophyllum ellenbergii* (Mor 111 Dic zub): of the 4 fertile individuals indicated, only one is from our own Molteno collection, the remaining 3 (plus 2 infertile individuals) are in the Fabre collection in Paris (this is the only reference to collections other than our own in this or any of the other tables in this volume).

Tab. 6a, b. (see previous page). Molteno ferns matrix, fertile & sterile species (abundance & frequency)

**Assemblages (taphocoenoses, TCs):** the 100 sampled Molteno TCs are arranged in stratigraphic sequence following the 6 recognised sedimentary cycles (members).

**Fern species:** the 16 genera & 37 species (fertile first, sterile following) are listed in classified sequence.

**Productive TCs (ferns):** 50 of the 100 TCs (exactly half) yield fern material.

**Abundance:** bold = % estimate made at site;
mild = individuals in curated collection (where <1%).

**Reference:** see And. & And. (2003) for sampling details.
### Tab. 8. Molteno ferns matrix: fertile specimens covered in the colour plates

**Matrix**: the figures within the matrix (with 5 exceptions) indicate numbers of fertile individuals covered in the colour plates; only 5 fertile indivs selected to show either overall morphology or venetian details, pls 102(2), 106(2), 146(4), 152(1–4), are included.

**Taphocoenoses (TCs)**: 12 TCs (of the 23 yielding ferns) are represented; one additional TC (Lut 311) is included with the infertile material.

**Taxa**: 7 genera, 16 species are represented.

**Taxa not covered (* & **)**: Elantodites joydeniorum (*): the 3 Bir 111 fertile indivs of this species (see Tab. 7 opposite) are insufficiently preserved to merit colour photography. Dictyophyllum ellenbergii (**): though a single fertile specimen from Mor 111 occurs in our collection, it is insufficient to be included in these plates (see also notes to Tab. 7).

**Reference palaeodemes (RPs)**: all but 3 of the 16 species are illustrated (fertile material) exclusively through individuals from the RPs; the exceptions being:

- Birtothites holmesii: represented by one additional SP (Aas 411);
- Elantodites turneri: represented by 3 additional SPs (Tel 111, Pen 222, Aas 111);
- E. kitchingii: represented by one additional SP (Ela 112).

**Holotypes**: around half (7 of 16) of the species are illustrated exclusively by the holotype (in most cases it is the only available specimen); in most other cases, the holotype is core to the coverage.

**Individuals**: a total of 41 individuals (3 per species on average) are represented.

<table>
<thead>
<tr>
<th>Matrix tables</th>
<th>Frequencies (TCs)</th>
<th>Abundance (individuals)</th>
<th>Infertile material covered in colour plates (5 indivs from 5 TCs)</th>
</tr>
</thead>
<tbody>
<tr>
<td>assemblages (taphocoenoses)</td>
<td>Deu. dep. (Tel 225)</td>
<td>A. dep. chevron (Kon 225)</td>
<td>A. dep. chevron (Kon 225)</td>
</tr>
<tr>
<td>Cal 111 Equ sp</td>
<td>1</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Bir 111 Sph 2sp</td>
<td>1</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Cyp 111 Dic clia</td>
<td>1</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Kan 112 Hei elo</td>
<td>1</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>* 111 Ast spA</td>
<td>1</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Tel 111 Hei elo</td>
<td>1</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Kom 111 Sph/Dic</td>
<td>1</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>* 222 Din 1</td>
<td>1</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>* 211/221 Ast 2sp</td>
<td>1</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Pen 222 Dic/Equ</td>
<td>1</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>* 311 Hei elo</td>
<td>1</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Ela 112 Equ sp</td>
<td>1</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Mor 111 Dic zub</td>
<td>1</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Hla 211 Dic 3sp</td>
<td>1</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>* 213 Dic elo</td>
<td>1</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Umk 111 Dic 2sp</td>
<td>1</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Mat 111 Dic dub</td>
<td>1</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Lit 111 Dic/Hei</td>
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<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Aas 111 Hei elo</td>
<td>1</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>* 411 Dic/Sph</td>
<td>1</td>
<td>1</td>
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</tr>
<tr>
<td>Ask 111 Equ sp</td>
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</tr>
<tr>
<td>Frequency (TCs)</td>
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<tr>
<td>Abundance (individuals)</td>
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</table>

**Note**: The table above shows the matrix of fertile specimens covered in the colour plates, with the following columns indicating frequencies and abundance of specimens, and the infertile material covered in colour plates. The data reflect the distribution of fern species across different taphocoenoses (TCs) and their representation in the collection, allowing for a comprehensive understanding of the diversity and coverage of the Molteno ferns matrix.
<table>
<thead>
<tr>
<th>Fertile fern species (only fertile material considered)</th>
<th>TCS</th>
<th>Indivs</th>
<th>Ref. TC (for Molteno)</th>
<th>Man-hours cleaving for Ref. TC</th>
<th>Indivs in RP</th>
<th>Rarity in Ref. TC</th>
</tr>
</thead>
<tbody>
<tr>
<td>Elantodites turneri</td>
<td>7</td>
<td>5</td>
<td>Ela 112</td>
<td>14</td>
<td>18</td>
<td>rare</td>
</tr>
<tr>
<td>* kitchingii</td>
<td>6</td>
<td>28</td>
<td>Kon 211/221</td>
<td>30</td>
<td>8</td>
<td>rare</td>
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<tr>
<td>Rooitodites pulchra</td>
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<td>7</td>
<td>Kon 211/221</td>
<td>30</td>
<td>4</td>
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</tr>
<tr>
<td>Bintodites holmesi</td>
<td>3</td>
<td>23</td>
<td>Bir 111</td>
<td>550</td>
<td>8</td>
<td>extremely rare</td>
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<tr>
<td>Asterotheca chevronervia</td>
<td>3</td>
<td>9</td>
<td>(Kon 223)</td>
<td>7</td>
<td>5</td>
<td>rare</td>
</tr>
<tr>
<td>Osmundopsis petiolatis</td>
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<td>6</td>
<td>Umk 111</td>
<td>400</td>
<td>3</td>
<td>extremely rare</td>
</tr>
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<td>Rooitodites integra</td>
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<td>18</td>
<td>Kan 111</td>
<td>30</td>
<td>17</td>
<td>rare</td>
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<tr>
<td>Asterotheca killickii</td>
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<td>11</td>
<td>Umk 111</td>
<td>400</td>
<td>9</td>
<td>very rare</td>
</tr>
<tr>
<td>Elantodites stuartii</td>
<td>2</td>
<td>4</td>
<td>Bir 111</td>
<td>550</td>
<td>3</td>
<td>extremely rare</td>
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<tr>
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<td>10</td>
<td>Aas 411</td>
<td>512</td>
<td>10</td>
<td>very rare</td>
</tr>
<tr>
<td>Dictyophyllum allenbergii</td>
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<td>4</td>
<td>Mor 111</td>
<td>12</td>
<td>4</td>
<td>rare</td>
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<td>Hla 213</td>
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<tr>
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<td>3</td>
<td>Bir 111</td>
<td>550</td>
<td>3</td>
<td>extremely rare</td>
</tr>
<tr>
<td>* joydeniorum</td>
<td>1</td>
<td>3</td>
<td>Bir 111</td>
<td>550</td>
<td>3</td>
<td>extremely rare</td>
</tr>
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<td>Dictyophyllum bremerense</td>
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<td>3</td>
<td>Tel 111</td>
<td>90</td>
<td>3</td>
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<tr>
<td>Drepanozamites dutolii</td>
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<td>2</td>
<td>Hla 213</td>
<td>60</td>
<td>2</td>
<td>very rare</td>
</tr>
<tr>
<td>Osmundopsis botryoides</td>
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<td>1</td>
<td>Pen 311</td>
<td>35</td>
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</tr>
<tr>
<td>* sp. cf. O. scalaris</td>
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<td>1</td>
<td>Kon 211/221</td>
<td>30</td>
<td>1</td>
<td>very rare</td>
</tr>
</tbody>
</table>

7 genera, 18 species

Tab. 9. Molteno fertile ferns: abundance & frequency

Genera & species: arranged according to decreasing frequency (TCs), then decreasing abundance (indivs).
Taphocoenoses (TCs): number of TCs in which the genus is known.
Individuals (indivs): total tally of fertile specimens from all TCs.
Reference taphocoenosis (Ref. TC): that TC yielding the best-sampled palaeodeme for the species.
Man-hours cleaving (for Ref. TC): see And. & And. 2003. (Tab. 1) for data.
Indivs in RP: see Tab. 7, this volume, for data.
Rarity (in Ref. TC): as measured in man-hours cleaving; see And. & And. 2003, Tabs 8 a, b; p. 13.
Rare: > indiv. per 1–5 man-hours (but <1% of TC).
Very rare: 1 indiv. per 5–49 man-hours.
Extremely rare: 1 indiv. per 50–499 man-hours.
Vanishingly rare: 1 indiv. in >500 man-hours.
### Tab. 10a

<table>
<thead>
<tr>
<th>Hierarchy</th>
<th>Molteno genera (fertile genera)</th>
<th>of 84 F</th>
<th>of 5 U</th>
<th>spp D</th>
<th>% A</th>
<th>my L</th>
<th>Prominence</th>
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<tbody>
<tr>
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<td>Cladophlebis*</td>
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<td>21</td>
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<td>88</td>
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<td>2</td>
<td>Asterotheca*</td>
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<td>3</td>
<td>12</td>
<td>1%</td>
<td>23</td>
<td>54</td>
</tr>
<tr>
<td>3</td>
<td>Dictyophyllum*</td>
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<td>3</td>
<td>10</td>
<td>-</td>
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<td>41</td>
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### Tab. 10a, b. Prominence (FUDAL), Molteno fern genera in Gondwana Triassic (GT) context

**Molteno genera**: all 16 genera (fertile & infertile included).

**FUDAL fingerprints**: see And. & And. 2003 (pp 26, 27) for definitions & discussion.

**F** (Frequency): of the 84 productive degree squares across Gondwana;

**U** (Ubiquity): of the 5 continents comprising Gondwana;

**D** (Diversity): number of species;

**A** (Abundance): the norm in Molteno TCs (not shown if <1%);

**L** (Longevity): longevity in millions of years (in GT).

**Prominence**: FUDAL totals, ranging widely from 88 down to 4.

**Arrangement**: Tab. 10a: genera in order of decreasing prominence;

Tab. 10b: genera in classified order (fertile genera first).
### Tab. II. Fern Hypodigm, Gondwana Triassic (GT) occurrences

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Cladophlebis sp. A
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Asterotheca sp. A
Alethopteris (cf. Asplenium nebbense)
Cladophlebis (Todites) roesserti
Stormbergia gardneri
Cladophlebis nebbenis
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concinna
“
(Todites) göppertiana
Sphenopteris lobifolia

Gleichenites sp.
Todites sp.
“ baldonii
Rienitsia colliveri
Danaeopsis fecunda
Gleichenites gallegoi
Thaumatopteris shirleyi

Dictyophyllum tenuifolium
“
spectabile
Cladophlebis indica
Goeppertella stipanicicii
Asterotheca rigbyana
Coniopteris harringtoni
Dictyophyllum rothi
“
tenuifolium
Thaumatopteris sp.
Goeppertella stipanicicii
Scleropteris grandis
Cladophlebis mendozaensis
“
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Asterotheca truempyi
Cladophlebis mesozoica
“
mendozaensis
Asterotheca falcata
“
menendezii
“
falcata
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menendezii
“
rigbyana
Chansitheca argentina
Rienitsia arondiana
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Danaeopsis fecunda
Tranquilia jalfinii

NAME

Tab. 11. Fern Hypodigm, Gondwana Triassic (GT) occurrences

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pl 177(3)
pl 177(6)
pl 177(4, 5)
pl 177(1, 2)
pl 2(12, 12a)
pl 8
pl 9
tf 2
pl 7(1)
tf 1
tf 12(a, b)

pl (1–5)
pl 1(6)
pl 1(8)
p 63(1, 2)
pl 1(a)
pl 1(b)
pl 1(c)
pl 1(d)
pl 1(e)
f 1(8–10), pl 2(14, 18, 19)
pl (1–3), tf3
pl 1(5)
f 1(13)
pl 6(3,4)
pl 6(5)
pl 7(2)
pl 1A, tfs E–K
pl 1B, tfs A–D
f 1, 19–21
f 38
f 16, 33, 35–36
fs 1–4
f 1(11–12), pl 3(30, 31)
f 1(13–14), pl 3(29, 32)
pl 2(26), pl 3(27)
f 1(1–6), pl 3(25, 26), pl 4(29,
34, 35)
f 1(7–10), pl 4(30–32)
f 1(11), f2(12), pl 3(8), pl 4(36)
f 2(16–20), pl 3(27), pl 4(33, 37)
f 2(13–15), pl 3(22, 23)
pl 3(24)
pl 1(2, 3), tf 1(A–C)
pl 2(10)

ILLUSTRATIONS

¥
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cf. Cladophlebis rosemariae
cf.
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evelynae
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cf. Asterotheca chevronervia
cf. Cladophlebis rosemariae
Cladophlebis katherineae
“
paucinerva

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Herbstopteris colliveri
Ogmos fecunda
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Dictyophyllum shirleyi

Dictyophyllum sp.
Goeppertella stipanicicii
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Rooitodites sp.
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Dictyophyllum sp.
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Nymboidiantum grandis
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Rooitodites argentina
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Cladophlebis sp. indet.
Ogmos fecunda
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IDENTIFICATION

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S T R E L I T Z I A 21 (2008)


## Tab. 11. Fern Hypodigm, Gondwana Triassic (GT) occurrences (cont.)

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| | | | | | | | | |
| 1956 | Lele | | | | | | | |
| 1960 | Fabre & Greber | Maseru | | Morija | Dictyophyllum ellenbergii | f s 2 pl 6, f 2, 3 | | |
| | | | | | | | | |
| 1882 | Feistmantel | S. Rewa/Tiki | PI 12 | Parvora Fm. (and equivs) | Parvora | Asplenium whitbyense | s 2 | pl 8(2, 3) | Cladophlebus sp.
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| | | | | | | | | |
| 1956 | Lele | | | | | | | |
| 1962 | Lele | | | Kamatland (loc. 9) | | | | |
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| 1956 | Lele | | | | | | | |
| 1969 | Lele | | | | | | | |
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| 1962 | Lele | | | | | | | |
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| 1956 | Bell | et al. | | | | | | |
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| 1985 | Retallack | | | | | | | |
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| 1990 | Retallack | | | | | | | |
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| 1971 | Retallack | | | | | | | |
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| 1983 | Retallack | | | | | | | |
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| 1990 | Retallack | | | | | | | |
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| 1980 | Retallack | | | | | | | |
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| 1982 | Playford et al. | | | | | | | |
| | | | | | | | | |
| 1986 | Shirley | | | | | | | |
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| 1995 | Retallack | | | | | | | |
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| 1982 | Playford et al. | | | | | | | |
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| 1982 | Playford et al. | | | | | | | |
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| 1986 | Shirley | | | | | | | |
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| 1995 | Retallack | | | | | | | |
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| 1982 | Playford et al. | | | | | | | |
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| 1986 | Shirley | | | | | | | |
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Tab. II. Fern Hypodigm, Gondwana Triassic (GT) occurrences

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Tab. 11. Fern Hypodigm, Gondwana Triassic (GT) occurrences (cont.)

See And. & And. 1983 (pp 74, 81–87), 1989 (p. 18), for general concept & layout details of our hypodigm tables.

Authors: all references including Gondwana Triassic (GT) fern illustrations are covered.

Subregions (degree squares): the geographic plotting unit on the GT ‘Geostrat’ distribution maps for each fern genus is at this scale.

Formation: the stratigraphic plotting unit on the ‘Geostrat’ maps.

Locality: whilst we have introduced a consistent hierarchical ‘locality’ usage for the Molteno, usage in the GT literature is quite variable.

Illustrations: includes all photos & pen sketches (aside from duplicates indicated by an asterisk) of ferns appearing in the literature.

Identifications: = as identified in the cited work;
other names = as identified in this work.
Konings Kroon
(Kon 211/221 Ast 2spp)
all BP/24/214
Elantodites kitchingii

Konings Kroon
(Kon 211/221 Ast 2a2pp)

PRE/F/2364 (figs 6, 7)
PRE/F/2363 (figs 4, 5)
PRE/F/10243 (figs 1–3)
Elantodites kitchingii

BP/2/4215 (figs 1–4)

BP/2/2365b (figs 5, 6)

PRE/F/20358b
Elanspruit
(Ela 112 Equ sp)
all PRE/F/13223

Elantodites kitchingii
pl. 49
OSMUNDALES
Elantodites kitchingii

Elandspruit
(Ela 112 Equ sp)

all PRE/F13222a

Elantodites kitchingii
Dictyophyllum Lindley & Hutton 1834

Synonym
Thaumatopteris (see Webb 1982).

Type species
Dictyophyllum rugosum Lindley & Hutton 1834
Yorkshire, Great Britain, Middle Jurassic.

Generic concept
A dipteridacean fern with pseudo-palmate fronds bearing pinnae variously deeply to fully divided (not spirally arranged on the main rachis) and venation comprising strong primary and secondary veins and a polygonal network of fine tertiary veins; with sori scattered or covering the lamina and sporangia with longitudinal slightly oblique annulus.

Generic characters
Fertile foliage: frond palmate, pinnatifid to pinnae; pinnae elongate, variously deeply to fully divided, margins entire to deeply lobed; venation of strong primary and secondary veins from which tertiary venation arises to form a fine network of square or polygonal mesh and/or free endings throughout the lamina; sori of irregular shapes, scattered or covering the lamina; sporangia with longitudinal slightly oblique annulus.

Sterile foliage: as for fertile frond but without sporangia.

Etymology
Dictyophyllum—in reference to the bifurcation of the primary rachis of the pseudo-palmate frond.

Global range: numerous species, Pangaea, M. Tr.–K.

Gondwana Triassic occurrence
Frequency (F): 12 degree squares (of the 84 across Gondwana).
Ubiquity (U): 3 continents (of 5 comprising Gondwana).
Diversity (D): 10 species.
Abundance (A): <1% (the norm in Molteno TCs).
Longevity (L): 16 myrs (lower Ladinian–upper Norian).

Colonisation success: FUDAL rating 12/3/10/-/16 = 41.

Endemism: fairly widespread.

Molteno occurrence
Frequency (F): 8 TCs (of the 100 sampled in the Molteno).
Diversity (D): 3 species.
Abundance (A): 31 indivs total, rare to extremely rare.

Habit: probably similar to Dipteris, the various extant species being of medium to rather large size, terrestrial, lithophytic or epiphytic ferns with long creeping stems

Preferred habitat: appears mostly to be associated with Heidiphyllum thicket.

Affiliation (fertile & sterile fronds)
The characteristic shape and venation of these fronds allows ready identification to genus even in the absence of fertile fronds.

Classification & comparison
Suprageneric classification (Dipteridaceae/Polypodiales)
The family Dipteridaceae is based on the single extant genus Dipteris (with ca 8 spp) which occurs from India through south-east Asia to northern Australia. Dictyophyllum is placed in this family based on similar frond morphology and sporangia to Dipteris.

Intergeneric comparison
Webb 1982 synonymised Thaumatopteris with Dictyophyllum. Hausmannia has similar venation but the lamina is suborbicular to reniform and not deeply dissected.

Gondwana Triassic occurrence (elaborated)
Dictyophyllum occurs more commonly in Triassic sediments elsewhere in Gondwana, e.g. Australia (Herbst 1979; Webb 1983; Holmes 2001) and South America (Herbst 1992, 1993) than in the Molteno Fm.

Comparisons beyond Gondwana Triassic
Extant ferns
Dictyophyllum is very close in frond and sporangial morphology to the only extant genus Dipteris (see above) in this family.

Rarity & quality of fertile Molteno material (Tab.18)
As for most of the Molteno fern species with fertile material, there occurs just a single specimen in our collections (from one of the three Dictyophyllum species) that shows this particularly clearly.

D. ellenbergii: the fertile individuals from Mor 111, Win 111 and one from Lut 311 show clear venation, but in no instance are the ?fertile zones sufficiently diagnostic to merit their inclusion in the colour plates.

D. bremerense: although three of the four frond fragments of this species from the Tel 111 SP show the enigmatic ?fertile zones along the midrib and principle veins, only PRE/F/17482 shows up clearly in colour (pl. 151).

Tab. 18. Dictyophyllum, Molteno occurrence

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<td>3</td>
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<td>Lut 311</td>
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<td>3</td>
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<tr>
<td>Win 111</td>
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<td>2</td>
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<td>Mor 211</td>
<td>4</td>
<td>2</td>
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<tr>
<td>Umk 111</td>
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<td>2</td>
<td>-</td>
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<tr>
<td>Qac 111</td>
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<td>2</td>
<td>-</td>
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<td>Mat 111</td>
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<td>1</td>
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<td>Aas 411</td>
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<td>12</td>
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<tr>
<td>Total TCs</td>
<td>1</td>
<td>4</td>
<td>1</td>
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<tr>
<td>Total indivs</td>
<td>4</td>
<td>9</td>
<td>3</td>
</tr>
</tbody>
</table>
Dictyophyllum ellenbergii Fabre & Greber 1960

Holotype
Specimen: MNHN Paris (catalogue number not given); Fabre & Greber 1960, pl. 6(2–5), tf. 3(A, B).
Assemblage: Mor 111 Dic odo, Morija.
Preservation: virtually complete frond, with counterpart; impression in thickly laminated, light olive-grey shale with poor cleavage.

Reference palaeodeme
Assemblage (TC): as for holotype.
Specimens: at least 5 indivs in Fabre collection, Paris; 1 indiv. (our collection), 74 fertile (2 intact, 2 partial), 2 sterile (2 partial); pl. 51 (1–3).
Note: both collections reflected in our tables.

Sister palaeodemes—3
Win 111 Hei elo: 2 indivs sterile (partial, frag.), pl. 51(6, 7).
Qac 111 Hei/Dic: 2 indivs sterile (frags), pl. 51(4, 5).
Lut 311 Hei elo: 3 indivs sterile (2 partial, 1 frag.), pls 52, 152(4).

Specific concept
A Dictyophyllum species with ca 10 pinnae up to 30 mm wide and with shallowly lobed margins.

Specific characters
Fertile foliage: frond pinnate; pinnae to ca 10, up to 30 mm wide and >110 mm long, margins with acute shallow lobes; sporangia sparse, in elongated sori along rachis and in spheroidal sori adjacent to lateral veins.
Sterile foliage: as for fertile but without sporangia.

Eponymy
ellenbergii—with reference to F. Ellenberger, missionary and palaeontologist from Morija, Lesotho, who discovered and collected from the type locality.

Comment & comparison
Webb (1983) placed this species with Dictyophyllum davidii since he regarded it as one end of the range as found in Australia. Holmes (2001) suggested it should be regarded as distinct as it was separated geographically and in time from D. davidii. We agree with Holmes and here retain it as a distinct species in the Molteno where it is distinguished by having fewer pinnae than D. davidii.

A good intact specimen from Lut 311, pl. 52, has deeper lobes than the D. ellenbergii specimens from Morija, but in pinnae width and venation it is closely similar. The small fragments from Win 111 and Qac 111 are placed here on the basis of the distance between the lateral veins (ca 5 mm) being less than for D. bremerense but also similar to D. davidii which has a distance of 4–8 mm.
**Dictyophyllum bremerense** Shirley 1898

**Lectotype**—designated by Herbst (1979).

**Specimen**: GSQ F166 (Shirley 1898, pl. 13, fig. 2)

**Assemblage**: Denmark Hill, UQ L85, Blackstone Fm., Ipswich Coal Measures, Queensland, Australia; Carnian, Late Triassic.

**Reference palaeodeme (RP)**

**Assemblage**: as for lectotype.

**Specimens**: ca 34 indivs.

**Sister palaeodemes**—3

Mat 111 Dic dub: 1 indiv. infertile (partial), pl. 53(1–3).
Tel 111 Hei elo: 3 indivs fertile (3 partial), 1 sterile (frag.), pls 151, 152(1–3).
Unk 111 Dic 2 spp: 1 indiv. infertile (frag.), pl. 53(4–6).

**Specific concept**

A *Dictyophyllum* species with ca 14 pinnae up to 60 mm wide and with deeply lobed margins.

**Specific characters** (based on Denmark Hill RP)

**Fertile foliage**: frond pinnatifid; pinnae ca 14 in number, up to 60 mm wide, >140 mm long, margins with shallow to deep lobes; sporangia in elongated sori along rachis and in spheroidal sori scattered or crowded on lamina.

**Sterile foliage**: as for fertile but without sporangia.

**Etymology**

bremerense—after the township of Bremer, near Ipswich, Queensland.

**Comment & comparison**

Webb (1982) distinguished *Dictyophyllum bremerense* from *D. davidii* by the greater size and deeper lobing of the pinnules and particularly by the spacing of the lateral segments (lobes). They show a distance of 8–14 mm between the lateral veins as apposed to 4–8 mm in *D. davidii*. Both Tel 111, pls 151, 152(1–3), and Mat 111, pl. 53(1–3), yield specimens that show deep lobes with the distance between the lateral veins being 7.5–8.5 mm and 9–11 mm respectively. The small fragment from Unk 111, pl. 53(4–6), consisting of a single isolated lobe, fits best in this species.

From the Tel 111 SP the enigmatic ?fertile zones along the midrib and principle veins, only PRE/F/17482 shows up clearly in colour (pl. 151).

**General comment on fertile Dipteridaceae**

The supposed fertile Dipteridaceae from the Gondwana Triassic remain enigmatic. Apparently fertile specimens from the Middle to Late Triassic across Gondwana have been illustrated in several papers, e.g. Fabre & Greber 1960 (Morija, Molteno Fm., South Africa), Webb 1982 (Denmark Hill, Ipswich Fm., Queensland), Herbst 1993 (Llantenes and Paso Flores, Argentina), Holmes 2001 (Nymboida Coal Measures, Basin Creek Fm., N.S.W). In none of these works has the morphology of the sporangia been demonstrated through photos or pen sketches and nowhere has it been described.

Our own Molteno material is similarly enigmatic. We list a total of four fertile individuals from Morija (Mor 211) and three from Telernachus Spruit (Tel 111), Tab. 7. The best preserved of those from Tel 111 is illustrated in our colour plates, pl. 151(1–3). The general arrangement and appearance of the apparent fertile specimens from the Molteno is like that from elsewhere in the Gondwana Triassic with no evident sporangia preserved. Close up photos, pl. 151(3), show an amorphous structure taken to be sori, but which might possibly also be fungal or due to some other organism.

The extant Dipteridaceae are represented by the single genus *Dipteris*. This has clear sporangia, with well-developed longitudinal, slightly oblique annuli clustered into ex-indusiate sori scattered across the laminae (Kubitzki 1990). In the non-Gondwana Triassic fossil record, the material from the Yorkshire Jurassic fits very well with the extant *Dipteris*: Harris (1961) includes excellent sketches of *Dictyophyllum rugosum* sporangia sparsely or densely spread across the laminae with the characteristics oblique annulus.
**Dictyophyllum shirleyi** (Herbst 1979) Webb 1982

**Holotype**
*Specimen:* UQ 64280; Herbst 1979, pl. 29 (10), fig. 5 (14, 18).
*Assemblage:* UQ L 3652, Ipswich, Blackstone Stage, Ipswich Coal Measures, Queensland, Australia; Carnian, Late Triassic.

**Reference palaeodeme**
*Assemblage* (TC): Aas 411 Dic/Sph, Aasvoëlberg.
*Specimens:* 12 indivs sterile (5 partial, 7 frags), pl. 54.

**Sister palaeodemes**—nil.

**Specific concept**
*A Dictyophyllum* species with an unknown number of pinnae up to 120 mm wide and with deeply lobed margins.

**Specific characters**
*Fertile foliage:* unknown
*Sterile foliage:* frond pinnatifid; pinnae of unknown number, up to 120 mm wide, margins deeply lobed.

**Eponymy**
*shirleyi*—after John Shirley, a pioneer Australian palaeobotanist.

**Comment & comparison**
This species is far larger than any of the other species described from the Gondwana Triassic. Our specimens compare well with the type although they are a little smaller. *Dictyophyllum shirleyi* is known from UQ Locality 3652, near Ipswich, Australia, which has also yielded 9 individuals of *D. bremerense*. Webb (1982) considered the possibility that all specimens may belong to the one species. However, he concluded that two species were represented. That decision is supported by the reasonably complete pinnae, PRE/F/12091a,b (pl. 54), from Aas 411 in the Molteno.
Morija
(Mor 111 Dic zub)
BP/2/7039 (figs 1–3)

Qachasnek
(Qac 111 He/Dic)
PRE/F/1701 (figs 4, 5)

Winnaaspruit
(Win 111 Hei elo)
BP/2/8951 (figs 6, 7)

 Dictyophyllum ellenbergii
pl. 51

POLYPODIALES
POLYPODIALES

Dictyophyllum ellenbergii

Lutherskop
(Luf 311 HeiDic)
Matatiele
(Mat 111 Dic dub)
BP/2/2996 (figs 1–3)

Umkomaas Valley
(Umk 111 Dic 2spp)
PRE/F/412 (figs 4–6)
Aasvoldberg
(Aas 411 Dic/Sph)

all PRE/F12091a or b
**Cladophlebis** Brongn. 1849

**Type species**
Cladophlebis albertsii (Dunker 1846) Brongn. 1849

**Germany; Early Cretaceous.**

**Generic concept**
An (?)osmundalean fern based on sterile bipinnate fronds bearing broadly attached and variously decurrent pinnules with prominent midvein and lateral veins forking usually once or twice.

**Generic characters**
Sterile foliage. Frond bipinnate, size variable; pinnules widely to closely spaced; pinnules separated to base, broadly attached and variously decurrent; base occasionally slightly lobed or acroscopically, margins entire to slightly lobed or serrate, parallel-sided to slightly tapering, straight or variously falcate; *venation* with prominent midvein usually persistent almost to the apex; lateral veins generally alternate, unforked (rarely) to forking 1 or 2 (rarely 3) times.

**Classification & comparison**

<table>
<thead>
<tr>
<th>Tab. 19. <em>Cladophlebis</em>, Molteno occurrence</th>
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<tbody>
<tr>
<td>Cladophlebis assemblages (phycopollenites)</td>
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<td>Ken 111</td>
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<td>Cal 211</td>
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<tr>
<td>Total TCs</td>
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<td>Total indivs</td>
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</table>

**Global range:** numerous spp., Pangaea, Tr.–K.

**Gondwana Triassic occurrence**

- **Frequency (F):** 32 degree squares (of the 84 across Gondwana).
- **Ubiquity (U):** 4 continents (of 5 comprising Gondwana).
- **Diversity (D):** 21 species.
- **Abundance (A):** 5% (the norm in Molteno TCs).
- **Longevity (L):** 26 my (lower Spathian–upper Norian).
- **Colonisation success:** FUDAL rating 32/4/21/5%/26 = 88.
- **Endemism:** very widespread.

**Molteno occurrence**

- **Frequency (F):** 36 TCs (of the 100 sampled in the Molteno).
- **Diversity (D):** 8 species.
- **Abundance (A):** 20% to 1 indiv., co-dominant to very rare.

**Affiliation (fertile & sterile fronds)**

- **Cladophlebis** is based solely on sterile pinnules and is regarded as a morpho-genus. Only the presence of sterile and fertile pinnules occurring on the same frond/plant will allow for accurate affiliation. In the Molteno assemblages, affiliations with Cladophlebis are suggested for Osmundopsis, Asterotheca and Birtodites (see relevant text under genus pages). Sterile fronds from Antarctica, placed in *Cladophlebis* by Taylor et al. (1990) were later included in the genus *Osmunda* as *O. claytoniites* Phipps et al. (1998) (see also text under Osmundopsis).

**Classification & comparison**

- **Intergeneric classification**

  The genus *Cladophlebis* was erected by Brongniart (1849) for sterile fern fronds. As a morpho-genus, it is now restricted to the Mesozoic fronds (Boureau & Doubinger 1975) with similar fronds from the Palaeozoic being placed in *Pecopteris*. The fertile genera Todites, Eboracia, Dicksonia, Klukia and Kyldkipetris all have *Cladophlebis*-type sterile foliage (Boureau & Doubinger 1975). In the Molteno, the new fertile genera Rootoidtes and Elantodites have sterile foliage that in the absence of fertile material would be placed in *Cladophlebis*. The fertile genus *Asterotheca* has sterile foliage that, in the Gondwana literature, has been placed variously in *Cladophlebis* or *Pecopteris*. 

Cladophlebis

*Cladophlebis* Brongn. 1849

**Type species**
Cladophlebis albertsii (Dunker 1846) Brongn. 1849

**Germany; Early Cretaceous.**
Interspecific comparison

Numerous _Cladophlebis_ species have been described in the Gondwana Triassic literature (see Tabs 4, 11) based often on fragmentary or inadequately illustrated material. The revisions of the genus by Frenguelli (1947) and Herbst (1971, 1978) have not clarified the taxonomy and nomenclature. For example, _Cladophlebis australis_ (Morris) Walkom (following Herbst 1978) is particularly confused, due to the selection of a new type and disregard for the original descriptions and illustrations by Morris (1845). We had great difficulty in relating much of our Molteno material with earlier described taxa, mostly those from Australia and South America. The genus needs further revision, especially in the Gondwana Triassic (GT), based on more extensive collections and well-preserved material.

For the Molteno, we have separated the _Cladophlebis_ fronds into morpho-species based on the better preserved material and on TCs with larger collections. The less well-preserved fossils or smaller collections or very fragmentary fronds from the Molteno are referred where possible to a Molteno morpho-species or noted as sp. indet. We have endeavoured to identify our material with previously described taxa, e.g. _C. paucinerva_ Holmes (2003) from Nymboida was found to agree well with one of the Molteno species.

After careful and comprehensive study of the literature and based on our extensive Molteno collections we have erected an additional seven new _Cladophlebis_ species. We therefore follow a similar approach to that of Holmes (2003), who from his large collection of ferns made over 30 years from Nymboida in Australia, has described six new species of _Cladophlebis_ and an additional three as _Cladophlebis_ sp. A, B and C, with comparisons (where relevant) being made, with previously described material.

Amongst the eight Molteno _Cladophlebis_ species, _C. paucinerva_, with a short midvein and few once-forked lateral veins, is separated from _C. rosemariae_ by the longer midvein and the greater number of once-forked lateral veins. The remaining six species, all with twice-forking lateral veins, with the exception of the very much smaller _C. felixii_, are more difficult to distinguish.

From Umk 111, a large collection of sterile fronds share certain common characters, i.e. all have a thin rachis (1.5–3.0 mm), are smaller (300 mm long) and have the common venation character of twice-forking lateral veins. They have been separated into three species, _C. katherineae_, _C. moltenensis_ and _C. barbara_, based mainly on differences in pinnule characters.

From other localities a further two species of _Cladophlebis_ occur that have a thick rachis (4–5 mm), are larger fronds (400 mm long or more) and with twice- (or three-times) forked lateral veins. _C. evelynae_ is distinguished by the thrice-forked lateral veins. The lateral veins in _C. janetae_ are more strongly arched than in the _Cladophlebis_ group from Umk 111.

Where only a few individuals (often fragmentary) occur at a locality, identification is less certain. Most of these, with twice-forked lateral veins, have been identified as close to _C. katherineae_, _C. moltenensis_ or _C. janetae_, or, if with once-forked lateral veins, as _C. rosemariae_.

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### _Cladophlebis_ pinnule key

As far as possible the pinnule were drawn from the mid-frond & mid-pinnae areas.
**Cladophlebis paucinerva** Holmes 2003

**Holotype**

Specimen: AMF120979, Australian Museum Sydney.

**Assemblage**: Reserve Quarry, Nymboida, Basin Creek Fm., Nymboida C.M.; Middle Triassic.

**Preservation**: small partial frond, impression in grey sandy shale.

**Reference palaeodeome**


**Specific concept**

A *Cladophlebis* species bearing small roundly oblong pinnules (L:W ratio ca 2:1) with entire margins and weakly-developed midvein with ca 1 or 2 pairs of once-forked lateral veins.

**Specific characters**

**Sterile foliage**: frond very small, estimated length 50 mm, bipinnate, rachis very thin (1 mm wide), pinnules small, 3–8 mm long and 1.5–3.0 mm wide, L:W ratio ca 2:1; margin entire; midvein slightly undulate, forking well before apex; lateral veins in 2–4 pairs, weakly developed, forking once.

**Specific characters**

**Sterile foliage**: frond very small, 3–8 mm long and 1.5–3.0 mm wide, L:W ratio ca 2:1; margin entire; midvein slightly undulate, forking well before apex; lateral veins in 2–4 pairs, weakly developed, forking once.

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**Comment & comparison**

*Cladophlebis paucinerva* is distinguished from other *Cladophlebis* species by the small size, the weakly-developed midvein and the few lateral veins that fork only once.

This species, although well represented by a total of 7 palaeodeomes from the Molteno is based on limited individuals and small fragments. The venation is very similar to the Australian specimens but generally the Molteno fronds are larger in size. Two specimens from Bir 111 (PRE/F:15604a,b; BP/2:4682) are placed here based on their diagnostic venation but in size they are very much larger. The Umk 111 specimen referred to *Sphenopteris komisofolia* by Du Toit (1927, tf. 12A, B) is best placed in *C. paucinerva*.

Cell structure is observed from a few localities, illustrated here from Gre 121, pl. 56(4, 5). This is similar to that occurring in *C. katherinae*, pl. 60(2, 3), and *C. mollenensis*, pl. 62(2), from Umk 111.

**Cladophlebis rosemariae** H.M. And. & J.M. And., sp. nov.

**Holotype**

Specimen: PRE/F:13570a,b; pl. 57(2–4).

**Assemblage**: Pen 321 Dic/Ris: Peninsula (Rissikia Chert).

**Preservation**: partial frond; impression in thickly laminated, medium grey shale with poor cleavage.

**Reference palaeodeome**

Assemblage (TC): as for reference specimen.

**Specific characters**

A *Cladophlebis* species bearing medium oblong pinnules (L:W ratio ca 2.5:1) with entire margins and gracile slightly undulate midvein and with ca 6 pairs of once-forked lateral veins.

**Comment & comparison**

*Cladophlebis rosemariae* has once-forked lateral veins as in *C. paucinerva*, but differs by the long midvein and the greater number of lateral veins. The other Molteno *Cladophlebis* species all have double-forking lateral veins. Sterile fronds with once-forking lateral veins similar to *C. rosemariae* are associated with *Asterotheca dewinteri* at Hla 213, with *Rooitodiales* integra and also with the fertile fronds of *Asterotheca nymboidensis* as described by Holmes (2001). *Cladophlebis rosemariae* from Hla 212 is closely comparable with the sterile foliage of *Asterotheca dewinteri* and may be affiliated. To date no fertile material is known from that TC.

**Eponym**

*rosemariae*—for Heidi’s sister Rosemarie Schwyzzer who helped with the collection of Molteno fossils in the early 1970s.

**Comment & comparison**

*Cladophlebis rosemariae* has once-forked lateral veins as in *C. paucinerva*, but differs by the long midvein and the greater number of lateral veins. The other Molteno *Cladophlebis* species all have double-forking lateral veins. Sterile fronds with once-forking lateral veins similar to *C. rosemariae* are associated with *Asterotheca dewinteri* at Hla 213, with *Rooitodiales* integra and also with the fertile fronds of *Asterotheca nymboidensis* as described by Holmes (2001). *Cladophlebis rosemariae* from Hla 212 is closely comparable with the sterile foliage of *Asterotheca dewinteri* and may be affiliated. To date no fertile material is known from that TC.

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Cladophlebis katherineae H.M.And. & J.M.And., sp. nov.

**Holotype**
- *Specimen*: BP/2/409'A'; pl. 59(1–3).
- *Assemblage*: Umk 111 Dic 2pp, Umkomaas Valley.
- *Preservation*: partial frond; compression in thinly laminated, carbonaceous (cuticle), moderately baked, dark grey shale with good cleavage.

**Reference palaeodeme**
- *Assemblage (TC)*: as for holotype.
- *Specimens*: 17 indivs (3 intact, 2 partial, 12 frags), pls 59, 60.

**Sister palaeodemes—6**
- Boe 111 Lep sto: 2%, 8 indivs (3 intact, 2 partial, 3 frags).
- Kom 111 Sph Dic: 3% (partial to frags).
- Hla 213 Dic elo: 5 indivs (4 partial, 1 frag).
- Gre 111 Sph pon: 2 indivs (2 frags).
- Bir 211 Sph 2pp: 1 indiv. (1 frag.).
- Ken 111 Dic era: 1 indiv. (1 frag).

**Specific diagnosis**
A *Cladophlebis* species bearing medium broadly lanceolate pinnules (L:W ratio ca 2.5:1) with entire margins and gracile straight midvein with ca 6 pairs of twice-forked lateral veins.

**Specific characters**
- **Sterile foliage**: frond small, bipinnate, estimated length ca 150 mm, rachis thin (1.3 mm wide), pinnule well spaced; pinnules broadly lanceolate, with a variously contracted basiscopic base and decurrent acroscopic base, 7–9 mm long and 3–4 mm wide, L:W ratio ca 2.5:1, margin entire; midvein gracile straight; lateral veins in ca 6 pairs, usually forking twice.

**Eponym**
Katherine—named after Heidi’s artist friend Katherine Ambrose who helped us collect Molteno fossils in the 1990s.

**Comment & comparison**
*Cladophlebis katherineae* differs from the somewhat similar Molteno species: *C. moltenensis* by its smaller size, by the presence of the acrosopic decurrent base on the pinnules and the L:W ratio; *C. barbara* by the more widely spaced pinnules and pinnules and a lower L:W ratio of the pinnule.

Some specimens (e.g. PRE/F/6624) are close to *C. katherineae*, 6 pairs, twice-forked lateral veins. Some fronds, e.g. pl. 64, have a lower L:W ratio and approach *C. barbara* but are here included in *C. moltenensis*.

A specimen of *C. katherineae* from the type locality, Umk 111, was identified by Du Toit (1927, tf. 1) as *C. (Todites) gippertiana*, a northern hemisphere taxon.

*C. katherineae* is also close to *C. mesozoica*, especially to the lectotype nominated by Herbst (1971) and illustrated by Frenguelli (1947, pl. 8A), but differs by the more parallel lateral veins and the decurrent acroscopic pinule base.

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Cladophlebis moltenensis H.M.And. & J.M.And., sp. nov.

**Holotype**
- *Specimen*: BP/2/9806; pl. 61.
- *Assemblage*: Umk 111 Dic 2pp, Umkomaas Valley.
- *Preservation*: partial frond; compression in thinly laminated, carbonaceous (cuticle), moderately baked, dark grey shale with good cleavage.

**Reference palaeodeme**
- *Assemblage (TC)*: as for holotype.
- *Specimens*: ca 50 indivs (2 ca complete, 8 intact, ca 40 partial to frags), pls 61–64.

**Sister palaeodemes—5**
- Tin 131 Hei/Ast: 40%, 14 indivs (2 intact, 8 partial, 4 frags).
- Cal 211 Hei elo: 9 indivs (1 intact, 2 partial, 6 frags).
- Maz 211 Hei/Dic: 2 indivs (2 partial).
- Ken 111 Dic era: 2 indivs (1 intact, 1 frag.).
- Pen 211 Dic/Equ: 1 indiv. (partial).

**Specific diagnosis**
A *Cladophlebis* species bearing medium lanceolate pinnules (L:W ratio ca 3–4:1) with undulate margins and undulate midvein with ca 6 pairs of twice-forked lateral veins.

**Specific characters**
- **Sterile foliage**: frond medium, bipinnate, estimated length ca 250 mm, lanceolate, rachis thin (2 mm wide); pinnule short, alternate; pinnules 12–14 mm long and 3–4 mm wide, L:W ratio of 3–4:1, margin undulate; midvein undulate; lateral veins in ca 6 pairs, usually forking twice.

**Eponym**
Moltenensis—with reference to the occurrence of the species in the Molteno Fm.

**Comment & comparison**
*Cladophlebis moltenensis* is close to both *C. katherineae* and *C. barbara*, but differs by the undulate margins and the greater length to width ratio of the pinnule and by the acrosopic base not being strongly decurrent.

In the distal and apical pinnules of PRE/F/9808, the shorter midvein tends to become sinuous with the pinnules resembling those of *C. sinuata* Holmes (2003) from the Nymboida flora. Most other specimens of *C. moltenensis* have larger pinnules and straight veins. Some fronds, e.g. pl. 64, have a lower L:W ratio and approach *C. barbara* but are here included in *C. moltenensis*.

On some specimens where the cuticles have been bleached by weathering, the venation and some cell structure shows up very clearly, e.g. PRE/F/9802, pl. 62(2) and PRE/F/9808’Y’, pl. 63(3). Three virtually identical fronds labelled ‘X’, ‘Y’ and ‘Z’ are preserved together on a slab (pl. 63), which suggests they may have originated from the same parent plant.
**Cladophlebis barbara** H.M. And. & J.M. And., sp. nov.

**Holotype**

*Specimen:* PRE/F/9818; pls 65, 66.
*Assemblage:* Unk 111 Dic 2 spp, Unkomaas Valley.
*Preservation:* almost complete frond; compression in thinly laminated, carbonaceous (cuticle), moderately baked, dark grey shale with good cleavage.

**Reference palaeodeme**

*Assemblage* (TC): as for holotype.
*Specimens:* 6 indivs (1 ca complete, 1 intact, 3 partial, 1 frag.), pls 65–68.

**Specific diagnosis**

A *Cladophlebis* species bearing medium, roundly oblong pinnules (L:W ratio ca 2.5:1) with entire margins and fairly straight midvein with 6 pairs of once- to twice-forked lateral veins.

**Eponymy**

*barbara*—for Heidi’s sister Barbara Schwezyer who helped us collect Molteno fossils in the early 1970s.

**Comments & comparisons**

The holotype is an almost complete frond, the upper part being illustrated on pl. 65(1), the lower part on pl. 66(1).

*Cladophlebis barbara* differs from the somewhat similar Molteno species, *C. moltenensis* and *C. katherineae* by the slightly larger frond size, the closely-spaced, elongated parallel-sided pinnae and the L:W ratios of the pinnae being 4:1. The *Cladophlebis* fronds from Kon 211/221, pls 69, 70, are placed provisionally in *C. barbara*.

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**Cladophlebis janetae** H.M. And. & J.M. And., sp. nov.

**Holotype**

*Specimen:* BP/2/4292a,b; pls 71(2, 3), 72(1).
*Assemblage:* Aas 111 Hei elo, Aasvoëlberg.
*Preservation:* partial frond, part and counterpart; impression in thinly laminated, medium grey shale with moderate cleavage.

**Reference palaeodeme**

*Assemblage* (TC): as for holotype.
*Specimens:* 20% of assemblage (2 intact, partial, to frags), pls 71, 72.

**Specific diagnosis**

A *Cladophlebis* species bearing large lanceolate pinnules (L:W ratio ca 3–4:1) with undulate margins and straight tapering midvein with 8 pairs of twice-forked lateral veins.

**Eponymy**

*janetae*—named for our dear friend, the late Janet Fatti (née Cronje), who assisted with the collection of Molteno fossils from the type locality in the early 1970s.

**Comment & comparison**

*Cladophlebis janetae* is distinguished from the similar *C. katherineae* by having a thicker rachis and strongly arching veins that reach the margin at 60°.

Some specimens, e.g. pl. 72(2), have slightly lobed pinnules and tend towards tripinnatifid, with a slightly winged base and come close to *Parsophyllum*.

*C. australis sensu stricta* Morris (1845) is similar to *C. janetae* in pinnule L:W ratio and twice-forking lateral veins, but differs by the entire pinnules with slightly contracted acroscopic bases.

*Cladophlebis copiosa* from the Potrerillos Fm., South America, (Frenguelli 1947) appears to have similar venation but the small portion of frond illustrated as the type specimen makes comparison difficult.

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**Cladophlebis**

**Pinnules**

- **Size:** medium
- **Shape:** roundly oblong
- **Margin:** entire
- **Midvein:** fairly straight
- **Lat. veins:** ca 6 pairs, once- to twice-forked

**Cladophlebis barbara**

- **Pinnae:** closely-spaced
- **L:W ratio:** 4:1
- **Margins:** entire
- **Midvein:** fairly straight
- **Later. veins:** in ca 6 pairs, forking once or twice.

**Cladophlebis janetae**

- **Pinnae:** closely-spaced
- **L:W ratio:** 3–4:1
- **Margins:** undulate
- **Midvein:** straight tapering
- **Later. veins:** in ca 8 pairs, forking twice.
**Cladophlebis felixii** H.M. And. & J.M. And., sp. nov.

**Holotype**
*Specimen*: BP/2/521; pl. 76(1–5).
*Assemblage*: Umk 111 Die 2app, Umkomaas Valley.
*Preservation*: partial frond; compression in thinly laminated, carbonaceous (cuticle), moderately baked, dark grey shale with good cleavage.

**Reference palaeodeme**
*Assemblage* (TC): as for holotype.
*Specimens*: 2 indivs (1 intact, 1 partial), pl. 76.

**Sister palaeodemes**—nil.

**Specific diagnosis**
A *Cladophlebis* species bearing small to medium, roundly oblong pinnules (L:W ratio up to ca 2:1) with entire margins and straight midvein with ca 6 pairs of twice-forked lateral veins.

**Specific characters**
*Sterile foliage*: frond small to medium, bipinnate, estimated length 200 mm, rachis up to 5 mm wide with numerous striations; *pinnae* opposite, slightly overlapping, attached at ca 90°; *pinnules* oblong, usually overlapping, small, 6–12 mm long and 3–5 mm wide, L:W ratio 2:1, margin entire, apex obtuse; *midvein* straight; *lateral veins* in ca 6 pairs, usually forking twice.

**Eponymy**
*felixii*—for Heidi’s brother, Felix Schwyzer, who helped us collect Molteno fossils in the early 1970s.

**Comment & comparison**
*Cladophlebis felixii*, represented by only two individuals, is distinguished from the other Molteno *Cladophlebis* species with double-forking lateral veins by the relatively broad rachis, smaller pinnule L:W ratio and the overlapping pinnules. Nothing similar has been described elsewhere from the Gondwana Triassic.

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**Cladophlebis evelynae** H.M. And. & J.M. And., sp. nov.

**Holotype**
*Specimen*: PRE/F/2502; pls 77, 78(3), 79(1–3).
*Assemblage*: Boe 111 Lep sto, Boesmanshoek Pass.
*Preservation*: large partial frond with almost complete apex; impression in thickly laminated, grey mudstone with poor cleavage.

**Reference palaeodeme**
*Assemblage* (TC): as for holotype.
*Specimens*: 3 indivs (1 intact, 2 partial), pls 77–79.

**Sister palaeodemes**—2
Ela 112 Equ sp: 2 indivs (intact), pl. 80.
Lit 111 Die/Hei: 1 indiv. (1 frag.), PRE/F/5567.

**Specific diagnosis**
A *Cladophlebis* species bearing medium to large rhomboid pinnules (L:W ratio ca 1.6:1) with entire margins and straight tapering midvein with ca 6 pairs of lateral veins forking to three times.

**Specific characters**
*Sterile foliage*: frond large, bipinnate, estimated length at least 400 mm, rachis broad to at least 8 mm wide; *pinnae* alternate, well spaced, linear, L:W ratio 1.6:1; *pinnules* broad triangular-falcate, basiscopic base slightly contracted, acroscopic base strongly decurrent, 8–12 mm long and 5–7 mm wide, L:W ratio 1.6:1, margin entire to undulate, apex obtuse; *midvein* straight tapering; *lateral veins* in ca 6 pairs, forking to three times.

**Eponymy**
evelynae— for Heidi’s sister Evelyne Schwyzer who helped us collect Molteno fossils in the early 1970s.

**Comment & comparison**
Holmes (2003) described two sterile ferns, *Cladophlebis retallackii* and *Leconama stachyophylla*, both with similar pinnule shape and thrice-forking lateral veins as in *C. evelynae*. *C. retallackii* differs from *C. evelynae* by the strongly arched lateral veins and the L:W ratio 2.5:1 of the pinnules. *Leconama stachyophylla* differs by the arching venation that lacks a midvein.

We have placed the fronds from Ela 112, (pl. 80), provisionally with *C. evelynae* although they are smaller, the pinnule L:W ratio is 1–1.5:1 and the pinnules have less-forking lateral veins.

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### Pinnules

- **Size**: small to medium
- **Shape**: roundly oblong
- **L:W ratio**: ca up to 2:1
- **Margin**: entire
- **Midvein**: straight
- **Lat. veins**: ca 6 pairs, twice-forked

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### Pinnules

- **Size**: medium to large
- **Shape**: broad triangular-falcate
- **L:W ratio**: ca 1.6:1
- **Margin**: entire
- **Midvein**: straight tapering
- **Lat. veins**: ca 6 pairs, forking to 3 times
Cladophlebis paucinerva

pl. 55

OSMUNDALES
Cladophlebis paucinerva

Hlatimbe Valley
(Ga 213 Dic elo)

PRE/F/7845 (figs 4–6)
PRE/F/7846
PRE/F/8681
PRE/F/19911
PRE/F/19912
PRE/F/19913

Greenvale
(Gre 121 Hei elo)
Cladophlebis rosemariae

PRE/F/1479

Hlatimbe Valley
(Hla 212 Dic 3spp)

PRE/F/13570a or b
(figs 2–4)
Holotype

Peninsula
(Pen 321 Dic/Ris)

PRE/F/20430b

PRE/F/1479

PRE/F/1481
Cladophlebis rosemariae

Koningskroon
(Kon 222 Dic odo)
Cladophlebis katherineae

Pl. 59

Umkomaas Valley
(Umk 111 Dic 2 spp)

BP/2/498a (figs 1–3)

PRE/F/393

OSMUNDALES
Cladophlebis katherineae

Umkomaas Valley
(Umk 111 Dic 2 spp)

BP/2551 (figs 1-4)

PRE/F/6438
Cladophlebis moltensis

pl. 61

Umkomaas Valley
(Umk 111 Dic 2spp)

all BP/2/9806
Holotype
Cladophlebis moltenensis

Umkomaas Valley
(Umk 111 Dic 2spp)

PRE/F/98/02 (figs 1, 2)
BP/2/500 (figs 3, 4)
Cladophlebis moltenensis

Osmundales

Umkomaas Valley (coll. 111 Dk 2596)

All specimens: 'x', 'y', 'z'

Pl. 63

Osmundales
Cladophlebis moltenensis

PRE/F/9820 (figs 1–3)

PRE/F/9819 (figs 4, 5)

Umkomaas Valley
(Umk 111 Dic 2spp)
Umkomaas Valley
(Umk 111 Dic 2sp)

both PRE/F9818
Holotype

Cladophlebis barbara
pl. 65

attaches to frond on 66(1)
Cladophlebis barbara

Umkomas Valley (Umk 111 Dic 2 spp)
all PRE/F/8818 Holotype
Cladophlebis barbara

Umkomas Valley
(Umk 111 Dic 2spp)

all PRE/F:9819
cf. Cladophlebis barbara

pl. 69

Konings Kroon
(Kon 21f Ast 2spp)
cf. *Cladophlebis barbara*

Konings Kroon
(Kon 211 Ast 2app)
Cladophlebis janetae

Aasvoëlberg
(Aas 111 Hei elo)

BP/2/4286
BP/2/4292b (figs 2, 3)
Holotype

1

2

3

4

x 1

x 1

x 5

x 5

BP/2/4282

OSMUNDALES
Konings Kroon (Kon 111 Dic odo)

Cladophlebis janetae
Cladophlebis janetae

Birds River
(Bir 111 Sph 2spp)

PRE/F/10704 (figs 1-3)

PRE/F/10707

PRE/F/10707 (figs 1-3)
Cladophlebis felixii

BP/2/521 (figs 1–5) Holotype

Umkomaas Valley
(Umk 111 Dic 2spp)
Cladophlebis evelynae

pl. 77

Boesmanshoek Pass
(Boe 111 Lep sto)

BP/2/2502
Holotype

attaches to pinnae at bottom right of frond below

frond fragment opposite, 78(3), attaches here
Boesmanshoek Pass
(Boe 111 Lap sto)

**PRE/F/2507** (figs 1, 2)

*attaches to top of frond fragment adjacent, 78(1)*

**PRE/F/2503**

*attaches to bottom of frond, 77(1a)*

**BP/2/2502**
Holotype
Cladophlebis evelynae

Boesmanshoek Pass
(Boe 111 Lep sto)

PRE/F/2502 (figs 1–3)
Holotype

PRE/F/2503

PRE/F/2503

x 2
Cladophlebis evelynae

Elandspruit
(Ela 112 Equ sp)

PRE/F/13250a  (x1)
PRE/F/13250b (figs 1-3)
PRE/F/13269b (figs 5, 6)

PRE/F/13250b (figs 5, 6)
Sphenopteris (Brongn.) Sternberg 1825

**Type species**
*Sphenopteris elegans* (Brongn.) Sternberg 1825

Silésie, Carboniferous (see Boureau & Doubinger 1975, p. 490; given as Altwasser, Waldenburg, Silésie).

**Generic concept**
An ?osmundalean fern based on sterile tripinnatifid to tripinnate fronds bearing ultimate pinnules variously lobed and contracted at base.

**Generic characters**
Sterile foliage: fronds tripinnatifid to tripinnate; pinnules entire to shallowly or deeply lobed, variously contracted at base; venation with prominent midvein, lateral veins alternate, single or once-forked.

**Etymology**
*Sphenopteris*—*spheno* (Gr), wedge-shaped; *pteris* (Gr), wing.

**Global range:** numerous species, Pangaea, D.–K.

**Gondwana Triassic occurrence**
- **Frequency (F):** 9 degree squares (of the 84 across Gondwana).
- **Ubiquity (U):** 3 continents (of 5 comprising Gondwana).
- **Diversity (D):** 4 species.
- **Abundance (A):** 5% (the norm in Molteno TCs).
- **Longevity (L):** 17 myrs (Spathian lower Carnian).

**Holotype**
*Sphenopteris annakatiae* H.M. And. & J.M. And., sp. nov.

**Species characters**
- **Sterile foliage:** frond tripinnate, estimated length up to 300 mm; primary pinnae opposite, up to 90 mm long, attached at a high angle to main rachis, bearing ca. 6–14 pairs of secondary subopposite elongate tapering secondary pinnae up to 15 mm long; pinnules alternate, ca. 4 mm long by 2 mm wide, apex obtuse, coalescing distally; a single vein enters the base, forked to three times and radiating to the margin or forming a short midvein with 4 lateral veins.

**Ecology**
*annakatiae*—named after our colleague and friend Anna Katherina Malleson née Benecke, who helped collect Molteno plant fossils in the early 1970s.

**Comment & comparison**
*Sphenopteris annakatiae* is of distinct morphology among the fern-like foliage in the Molteno Fm. It is distinguished from *S. speciosa* (Holmes 2003, occurring at Nymboida, Australia) by its tripinnate form.

**Classification & comparison**
- **Suprageneric classification**
  - This is a morpho-genus for sterile foliage that is particularly common in the Palaeozoic (see Bouroue & Doubinger 1975 for a comprehensive account).

**Intergeneric comparison**
The genus *Cladophlebis* is close to *Sphenopteris* but differs in being bipinnate, having pinnules broadly attached and variously decurrent and in venation pattern.

**Interspecific comparison (Gondwana Triassic only)**
*Sphenopteris speciosa* (Holmes 2003) from Nymboida, Australia, is the only form somewhat similar to the Molteno species described here. In the Gondwana Triassic, the genus *Sphenopteris* has been erroneously for *Dicroidium* foliage by Tenison-Woods (1883), Shirley (1898), Walkom (1917, 1928) and Jones & de Jersey (1947). These were individually listed by And. & And. (1983, Tab. 9, Hypodigm list) in their review of the *Dicroidium* genus in the Molteno Fm. *S. delicatula* Shirley (1898, pl. 10, f. 1) is possibly a true fern, while *S. lacunosa* Shirley (1898, pl. 15, f. 1) is too poor for identification. *S. eskensis* Walkom (1928, pl. 26, f. 3) has now been placed in the new genus *Walkomopteris* by Holmes & Anderson (2005).

From Tasmania, Johnston (1896) described two similar ferns as *Sphenopteris tasmanica* and *S. morrisiana*. Walkom (1925b) transferred *S. tasmanica* to *Cladophlebis*. Those specimens, in gross morphology, resemble some of the Molteno *Sphenopteris* material. However, Johnston’s descriptions do not closely match his illustrations and the type material is reported lost (Herbst 1978). In our hypodigm (Tab. 11), *S. tasmanica* and *S. morrisiana* are listed as sp. indet.
S. annakatieae
Konings Kroon
(Kon 211/22 Ast 2 ssp)

all BP/24208
Holotype

Sphenopteris annakatiae
pl. 81
?OSMUNDALES
Sphenopteris annakatiae

BP/2/4208
Holotype

PRE/F/2359 (figs 2, 3)

BP/2/4207 (figs 4, 5)

Konings Kroon
(Kon 211/221 Ast Zapp)

PRE/F/2351
Birmoltia intervenatus

H.M. And. & J.M. And., sp. nov.

Holotype
Specimen: BP/2: 4743a, b, pl. 83(1–3).
Assemblage: Bir 111 Sph 2pp, Birds River.
Preservation: intact frond, with counterpart; impression in thinly laminated, yellowish grey shale with very good cleavage.

Reference palaeodeme
Specimens: 11 indivs (1 intact, 3 partial, 7 frags), pls 83, 84(1–6).

Sister palaeodemones—3
Cal 111 Neo car: 20% of TC; 39 indivs (3 intact, 11 partial, 25 frags).
Lut 211 Equ sp: 2 indivs (1 partial, 1 frag.).
Kon 222 Dic odo: 1 indiv. (partial), pl. 84(7).

Specific diagnosis—as for genus.
Specific characters—as for genus.

Etymology
intervenatus—(Lat.) referring to the diagnostic interveinal striae.

Comment & comparison
Birmoltia intervenatus differs from all other Molteno ferns by the elongated pinnae, the double forking veins running close and parallel to the margin and by the characteristic interveinal striae. From the same TC (Bir 111) are two individuals placed in Cladophlebis janetae (pl. 75) that have somewhat similar double-forking lateral veins, but the pinnales are larger and more elongated and the interveinal striae are absent.

The curious and problematical feature of this taxon is the striae between the lateral veins. That this is a constant feature is supported by the occurrence of a single individual from Kon 222, pl. 84(7), and in fronds from Cal 111 and Lut 211. A possible interpretation is that these striae are resin canals. Dr Conrad Labandeira of the Smithsonian Institute, Washington D.C., who is studying plant/insect interactions from the Molteno Fm., concludes that they are neither damage from insect leaf mining nor from other insect activity (pers. comm. 2005).

Similar interveinal striae occur in Asterotheca chevronervia pinnales, which suggests that these two species could possibly be fertile and infertile representatives of some unnamed genus or family of ferns. Differences at species level are particularly evident in the nature of the venation. However, the two species occur together at only the Kon 222 TC.
Birmoltia intervenatus

Birds River
(Bir 111 Sph 2spp)

BP/2/4743a (figs 1–3)
Holotype

BP/2/4746

BP/2/4745b (figs 5, 6)
**?OSMUNDALES** Bromhead 1838

*Nymbopteron* Holmes 2003

**Type species**
*Nymbopteron dejerseyi* Holmes 2003
Reserve Quarry, Nymboida, Basin Creek Fm., Nymboida C.M., NSW, Australia; Ladinian, Middle Triassic.

**Generic concept**
An ?osmundalean fern based on sterile bipinnate fronds, with the first acroscopic pinnule always confluent between the primary and secondary axes to form a triangular wing.

**Generic characters**
*Sterile foliage: frond* bipinnate-bipinnatifid, small to large; *pinnae* with the first acroscopic pinnule always confluent between the main and pinna rachis (primary and secondary axes) to form a wing; the first basiscopic pinnule sometimes enlarged, triangular, rectangular, rounded or variously lobed, often attached between main and pinna rachis or directly to the main rachis; subsequent cladophleboid pinnules of even size and shape; *lateral veins* forking up to five times.

**Etymology**
*Nymbopteron*—nymbo, for Nymboida, the type locality; pteron (Gr.), referring to the winged shape of the first acroscopic pinnules.

**Global range:** 5 spp, Gondwana, Tr. (LAD–CRN).
*First:* *Nymbopteron dejerseyi* Holmes 2003. Reserve Quarry, Nymboida, Basin Creek Fm., Nymboida C.M.
*Last:* the Molteno species described here.

**Gondwana Triassic occurrence**
*Frequency (F):* 2 degree squares (of the 84 across Gondwana).
*Ubiquity (U):* 2 continents (of 5 comprising Gondwana).
* Diversity (D):* 5 species.
* Abundance (A):* ~<1% (the norm in Molteno TCs).
* Longevity (L):* 6 myrs (lower Ladinian–lower Carnian).
* Colonisation success:* FUDAL rating 2/2/5/-/6 = 15.
*Endemism:* widely disjunct (SAf, Aus).

**Molteno occurrence**
*Frequency (F):* 1 TC (of the 100 sampled in the Molteno).
* Diversity (D):* 1 species.
* Abundance (A):* 5 indivs, extremely rare.

**Classification & comparison**

**Intergeneric comparison**
*Nymbopteron* is unique in having the triangular wing between the main and pinna rachis (first and second axes). Holmes (2003) listed as *Nymbopteron*, fronds placed previously in *Lobifolia* and *Cladophlebis*. A similar triangular wing occurs in *Elantodites* in both the fertile and sterile fronds, but always between the second and third axes. See under *Elantodites* for a discussion on the sterile genus *Parsorophyllum* Lele.

**Interspecific comparison**
Holmes (2003) described four *Nymbopteron* species from Nymboida, Australia, of which *N. foleyi* and *N. rhomboidale* are close to the Molteno species while *N. uncinatum* and *N. dejerseyi* are more distant.
**Nymbopteron ephippiata** H.M. And. & J.M. And., sp. nov.

**Holotype**
Specimen: PRE/F/6369; pl. 85(1–3).
Assemblage: Umk 111 Dic 2 spp, Umkomaas Valley.
Preservation: fairly complete frond, compression in thinly laminated, carbonaceous (cuticle), moderately baked, dark grey shale with good cleavage.

**Reference palaeodeme**
Assemblage (TC): as for holotype.
Specimens: 5 indivs (1 ca complete, 3 intact, 1 partial), pls 85, 86.

**Sister palaeodemes**—nil.

**Specific diagnosis**
A Nymbopteron species with rhomboidal pinnules and no basiscopic pinnules attached to main rachis.

**Specific characters**
Sterile foliage: frond bipinnate, estimated length ca 250 mm; pinnae ca 50 mm long by 7 mm wide; pinnules rhomboidal, the first acroscopic pinnule confluent between the main and pinna rachis (first and second axis) to form a saddle-shaped wing, no basiscopic pinnules attached to main rachis; a single vein enters each pinnule and forks up to four times, radiating to the margin where each vein-ending forms a slight marginal tooth.

**Etymology**
ephippiata—ephippion (Gr.) a saddle, with reference to the saddle-shaped outline of the first acroscopic pinnules.

**Comment & comparison**
Nymbopteron ephippiata is close to *N. foleyi* and *N. rhomboidale* from Nymboida, Australia, but differs by the absence of basiscopic pinnules attached to or decurrent on the main rachis. The pinnules are similar in shape to *N. rhomboidale* but are smaller and with less complex venation. *N. foleyi* has smaller fronds, but larger more falcate pinnules. The characteristic finely toothed pinnule margin is not present in any of the four Nymboida species.

Occasional specimens of *N. ephippiata* show some of the first acroscopic pinnules detached from the main rachis, probably an artifact of preservation, pl. 86(6).
Nymbopteron ephippiata

pl. 85

OSMUNDALES

Umkomaas Valley
(Umk 111 Dic 2spp)

PRE/F/6369
(figs 1–3)
Holotype

PRE/F/6372a

see 86(2)

x 5
Nymbopteron ephippiata

Umkomaas Valley
(Umk 111 Dic 2spp)

PRE/F/6372a or b
(figs 1-4)

PRE/F/6370
(figs 5, 6)
? OSMUNDALES Bromhead 1838

**Parsorophyllum** Lele 1969

**Type species**

*R. indica* Lele 1969, Parsora, Madhya Pradesh, South Rewa Gondwana Basin, India, Parsora Stage; Anisian, Triassic.

**Generic concept**

An ?osmundalean fern based on sterile bipinnate to tripinnate fronds with the basal acroscopic pinnule lobe (or ultimate pinnule) forming a wing-like structure between the secondary and tertiary axes.

**Generic characteristics**

Sterile foliage: *frond* tripinnatifid to tripinnate; *pinnae* narrowly elliptic; basal acroscopic *pinnule* forming a triangular wing-like structure between junction of secondary and tertiary axes; following *pinnules* broad ovate, conjoining distally; *venation* with prominent midvein, lateral veins arching or straight and dividing to three times; in the basal acroscopic wing the proximal vein runs parallel to the secondary axis.

**Etymology**

*Parsorophyllum*—named after the Parsora locality in India.

**Global range:** 2 spp., Gondwana Tr., (ANI–CRN).

*First:* Parsorophyllum Lele 1969, Parsora, Madhya Pradesh, South Rewa Gondwana Basin, India; Parsora Stage.

*Last:* the Molteno species described here.

**Gondwana Triassic occurrence**

*Frequency (F):* 4 degree squares (of the 84 across Gondwana).

*Ubiquity (U):* 2 continents (of 5 comprising Gondwana).

*Diversity (D):* 2 species.

*Abundance (A):* 4% (the norm in Molteno TCs).

*Longevity (L):* 14 myrs (lower Anisian to lower Carnian).

*Colonisation success:* FUDAL rating 4/2/4%14 = 26.

*Endemism:* disjunct (SAf, Ind).

**Molteno occurrence**

*Frequency (F):* 4 TCs (of the 100 sampled in the Molteno).

*Diversity (D):* 1 species.

*Abundance (A):* 17% to 3 indivs, abundant to very rare.

**Affiliation** (fertile & sterile fronds)

We regard *Parsorophyllum* as a morpho-genus for the sterile fronds that are not clearly affiliated with fertile material, i.e. at Ela 111, Nuw 111 and Maz 111. At Kon 211/221 it has been affiliated (grade 3) with Elantodites *kitchingii*. At Ela 112, Pen 222 and Ask 111, sterile fronds with this morphology occurring with fertile fronds are identified as Elantodites *turneri* (similarly for *E. stuartii* at Bir 111).

**Classification & comparison**

**Intergeneric comparison**

Lele (1969) distinguished *Parsorophyllum*, with its characteristic winged structure, from otherwise similar fronds occurring in *Sphenopteris*, *Mariopteris*, *Callipteridium*, *Dicroidium* and *Lepidopteris*.

*Nymbopteron* is a morpho-genus erected by Holmes (2002) for sterile fern-like fronds with a distinct modified basal acroscopic pinnule always confluent between the main rachis and pinna rachis (primary and secondary axes of the frond) to form a triangular wing. A similar triangular wing is found in *Parsorophyllum* but this always occurs at the acroscopic junction of the secondary and tertiary axes.

Where sterile fronds with morphology similar to *Parsorophyllum* occur in close association with fertile fronds, we place them in *Elantodites*. Where only sterile fronds occur in a particular TC they are placed in the morpho-genus *Parsorophyllum*.

**P. africana**

BP/2/4193b
R2
x 1

BP/2/4209
pl. 88(1–3)

R2
x 1

BP/2/4209
pl. 88(4)
**Parsorophyllum africana** H.M.And. & J.M.And., sp. nov.

**Holotype**

*Specimen:* PRE/F/10252; pl. 87.

*Assemblage:* Kon 211/221 Ast 2spp, Konings Kroon (Rooipoort Donga)

*Preservation:* an intact fertile frond; impression in massive light grey shale with poor cleavage.

**Reference palaeodeme**

*Assemblage* (TC): as for holotype

*Specimens:* 17% of TC; 36 indivs (10 intact, 15 partial, 11 frags), pls 87–91.

**Sister palaeodemes**—3

Ela 111 Dic odo: 5 indivs (2 intact, 2 partial, 1 frag.).

Nuw 111 Dic zub: 5 indivs (2 intact, 3 frags).

Maz 111 Dic cra: 3 indivs (1 intact, 2 partial).

**Specific diagnosis**

A *Parsorophyllum* species with tripinnatifid to tripinnate fronds.

**Specific characters**

Sterile foliage: frond tripinnatifid to tripinnate, estimated length to at least 500 mm; pinnae up to 200 mm long and 60 mm wide; pinnules of bipinnate forms and pinnae of tripinnate forms with a wing-like expanded acroscopic base always present between junction of secondary and tertiary axes; pinnules lobed to deeply divided, L:W ratio of 4–5:1.

**Etymology**

*africana*—with reference to the species coming from Africa.

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Comment & comparison

This species differs from *Parsorophyllum indica* by being tripinnatifid to tripinnate and not bipinnate. Lele (1969) noted that ‘the basal posterior pin-nule receives veins directly from the main rachis’, a feature not present in the Molteno fronds.

At Ela 111, an incomplete frond occurs with a rachis 6 mm wide, probably indicating that some fronds reached a length greater than 500 mm. The two incomplete portions of a large frond occurring at Nuw 111 also suggest a similar size. In the reference palaeodeme (Kon 211/221), are numerous fronds but none are complete. The longest of these is 190 mm, pl. 90(5), while other fronds have a broad rachis of 5 mm or more, pl. 89(1–4).

The specimen on pl. 91 is provisionally included here although the frond is bipinnate and the pinnules are entire. If not for the distinctive wing on the acroscopic base, it could be placed in *Cladophlebis*. Other fronds from Kon 211/221 have been placed in *C. barbara*, pls 69, 70.

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**Etymology**

*africana*—with reference to the species coming from Africa.
Parsorophyllum africana

Pl. 87

Konings Kroon
(Kon 211/221 Ast Zapp)

Holoype

all PRE/F/10252

x 1

x 5
Konings Kroon
(Kon 211/221 Ast 2spp)

BP/2/4193b (figs 1–3)

BP/2/4209

see 89(4)
Parsorophyllum africana

**Konings Kroon**
(Kon 211/221 Ast Zapp)

PRE/F/2357

PRE/F/10251

PRE/F/10242

BP/2/4206

BP/2/4209
Parsorophyllum africana

Konings Kroon
(Kon 211/221 Ast 2spp)

all PRE/F/2311

pl. 91

OSMUNDALES
**STRELITZIA** 21 (2008) 181

**OSTMUNDALES Bromhead 1838**

**Stormbergia** Seward 1911

**Type species**
Stormbergia gardneri Seward 1911. Cyphergat (horizon unknown), Molteno Fm., Karoo Basin, S. Africa; Carnian, Triassic.

**Generic concept**
An ?osmundalean fern based on sterile bipinnate fronds bearing petiolate pinnules.

**Generic characters**
Sterile foliage: frond bipinnate to tripinnatifid; pinnae opposite, well spaced on rachis; pinnules petiolate, entire to deeply lobed, apices obtuse to broadly acute; venation with prominent midvein and ca 5 lateral veins which fork 1 or 2 times.

**Etymology**
Stormbergia—named after the Stormberg Mountains not far from the type locality.

**Global range**: 2 spp, Gondwana, Tr. (CRN)
First: Stormbergia rosliae (= ?Cladophlebis sp. A, Holmes 2003, figs 9A, C), Coal Mine Quarry, Nymboida, Basin Creek Fm., Nymboida C.M.
Last: the Molteno species described here.

**Gondwana Triassic occurrence**

- **Frequency (F)**: 3 degree squares (of the 84 across Gondwana).
- **Ubiquity (U)**: 2 continents (of 5 comprising Gondwana).
- **Diversity (D)**: 2 species.
- **Abundance (A)**: <1% (the norm in Molteno TCs).
- **Longevity (L)**: 7 myrs (Ladinian–lower Carnian).

**Colonisation success**: FUDAL rating 3/2/2/-/7 = 14.

**Endemism**: highly disjunct (SAf, Aus.)

**Molteno occurrence**

- **Frequency (F)**: 2 TCs (of the 100 sampled in the Molteno).
- **Diversity (D)**: 2 species.
- **Abundance (A)**: 3 indivs total, vanishingly rare.

**Classification & comparison**

**Intergeneric comparison**
Stormbergia has similar venation to Cladophlebis but differs by the petiolate base of the pinnules.

**Affiliation (fertile & sterile fronds)**
The affiliation of Stormbergia by association is possible with Osmundopsis petiolaris at Umk 111 and Cyp 111. However, an affiliation is also suggested between O. petiolaris and Cladophlebis moltenensis which occurs in great abundance at Umk 111 (Tab. 6)

**Comparisons beyond Gondwana Triassic**

- **Extant ferns**
  In the family Osmundaceae, Osmunda regalis (Roux 2003) has petiolate pinnules and venation similar to Stormbergia gardneri. Leptopteris fraseri (Andrews 1990) has deeply lobed petiolate pinnules similar to S. rosliae.
**Stormbergia gardneri** Seward 1911

**Holotype**
Species: 3694 Albany Museum, Grahamstown, South Africa; Seward 1911, pl. 14.
Assemblage: Cyphergat, Molteno Fm., Karoo Basin; Carnian, Late Triassic.
Preservation: intact frond; impression in thickly laminated dark grey shale with moderate cleavage.

**Reference palaeodeme**
Assemblage (TC): as for holotype.
Species: 2 indivs (the intact holotype and 1 pinnule), pl. 92(3).

**Sister palaeodemes**—
Umk 111 Dic 2spp: 1 indiv. (partial, BP/2:685, pl. 92(1, 2).

**Specific diagnosis**
A *Stormbergia* species with simple pinnules.

**Specific characters**
Sterile foliage: frond bipinnate, length >100 mm; pinnules opposite, well spaced; pinnules alternate, well spaced, petiole ca 0.5–3 mm long, broadly elliptic, apices obtuse to broadly acute; venation with prominent midvein, lateral veins ca 5, forking 1 or 2 times, reach margin at ca 45°.

**Eponymy**
gardneri—after Mr Gardner who collected the type specimen.

**Comment & comparison**
*Stormbergia gardneri* differs from *S. rosliae* below by the simple entire pinnules.

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**Stormbergia rosliae** H.M. And. & J.M. And., sp. nov.

**Holotype**
Species: PRE/F/22521, pl. 124(4–6).
Assemblage: Umk 111 Dic 2spp, Umkomaas Valley.
Preservation: pinna fragment, compression in thinly laminated, carbonaceous (cuticle), moderately baked, dark grey shale with good cleavage.

**Reference palaeodeme**
Assemblage (TC): as for holotype.
Species: 1 indiv. (partial), pl. 92(4–6).

**Sister palaeodemes**—nil.

**Specific diagnosis**
A *Stormbergia* species with deeply lobed pinnules.

**Specific characters**
Sterile foliage: frond assumed to be tripinnatifid, length unknown; pinnules opposite, well spaced, shortly petiolate (ca 0.3–0.5 mm long), ovate-elongate, deeply lobed, apices obtuse to broadly acute; venation with prominent midvein, lateral veins branch into each pinnule lobe.

**Eponymy**
rosliae—for Rösli Schwyzter, Heidi’s mother, in appreciation for much babysitting during our collecting trips in the 1970s and 1980s.

**Comment & comparison**
Distinguished from *Stormbergia gardneri* by the deeply lobed pinnules. Two specimens from Nymboida, Australia, referred to *Cladophlebis* sp. A by Holmes (2003, Fig. 9A, C) are closely comparable with *Stormbergia rosliae*. 
Cyphergat
(Cyp 111 Dic cra)

Umkomaas Valley
(Umk 111 Dic 2spp)

BP/2/685 (figs 1, 2)

Strombergia gardneri (figs 1–3)

Strombergia rosliae (figs 4–6)

PRE/F/22524

Stormbergia pl. 92

Umkomaas Valley
(Umk 111 Dic 2spp)

PRE/F/22521 (figs 4–6)

x 5
Nymboidiantum

Holmes 2003

Type species
Nymboidiantum glossophyllum (Tenison-Woods 1883) Holmes 2001 ‘Talbragar Mines’, near Ballimore, Talbragar River, NSW, Australia; Napperby Fm.; Ladinian, Middle Triassic.

Generic concept
A ?polypodialean fern based on sterile pinnate to bipinnate fronds bearing alternate to opposite elliptic, entire to deeply incised pinnules with contracted decurrent base and forking radiating veins but no midrib.

Generic characters
Sterile foliage: frond bipinnate or rarely pinnate; pinnules attached at ca 45°, alternate to opposite, elliptic with contracted decurrent base, margin entire, lobed or deeply incised; venation with 1 to 3 acutely decurrent veins entering pinnule base then forking up to four times, lateral veins radiating slightly to the lobes or apical margin.

Etymology
Nymboidiantum—contrived from the name of the type locality, Nymboida, Australia, and with reference to the similar extant fern, Adiantum.

Global range: 6 spp, Gondwana, Tr. (LAD–CRN).
First: Nymboidiantum glossophyllum (Tenison-Woods 1883) Holmes 2001; Reserve Quarry, Nymboida, Basin Creek Fm., Nymboida C.M.
Last: the Molteno species described here.

Gondwana Triassic occurrence


Molteno occurrence
Frequency (F): 6 TCs (of the 100 sampled in the Molteno). Diversity (D): 1 species. Abundance (A): 5% to 1 indiv., common to vanishingly rare.

Classification & comparison
Suprageneric classification
The similarities with the modern genera Adiantum and Asplenium suggest placement in the Polypodiales but no fertile fossil material is available for confirmation.

Intergeneric comparison
Palaeozoic: Holmes (2003) refers to 6 genera with similar gross morphology of pinnules and venation.

Triassic: Nymbiella Holmes (2003) has similarities but differs from Nymboidiantum in not having a constricted pinnule base and odontoperoid venation. Walkomiopteris Holmes & Anderson (2005) has pinnae constricted at the base but is a pinnate frond with a dichotomy of the primary axis. Dicroidium species like D. dubium and D. zuheri may have similar pinnules and venation but differ in having pinnules attached to the forked main rachis.

Jurassic to Tertiary: fronds with similar morphology to Nymboidiantum but with distinct petioles, have been placed in Adiantopteris by Boureau & Doubinger (1975).

Interspecific comparison
Holmes (2003) described 5 species of Nymboidiantum from Nymboida, Australia. The Molteno frond illustrated by And & And. 1983, pl. 9(1a, b) was placed in N. glossophyllum by Holmes 2003. It is here placed separately in the new species N. schwzyzeri below.

New Nymboidiantum combinations
Artabe et al. (1994) identified a fern from Paso Flores, Argentina, as Scleropteris grandis. This frond has pinnules and venation closely similar to Nymboidiantum and should be placed in that genus as a new combination rather than in Scleropteris, a Jurassic genus based on fossils from France: thus Nymboidiantum grandis (Artabe et al. 1994) comb. nov. Walkom (1928) described a frond from Bryden Fm., Esk, Australia as Neuropteridium moombraense. This frond has pinnules and venation closely similar to Nymboidiantum and should be placed in that genus as a new combination rather than in Neuropteridium, a northern hemisphere Triassic genus based on fossils from Germany: thus Nymboidiantum moombraense (Walkom 1928) comb. nov.

Comparisons beyond Gondwana Triassic
Extant ferns
The genera Adiantum and Asplenium have pinnules with similar contracted bases and radiating venation but are characterized by their sori.
**Nymboidiantum schwyzeri** H.M.And. & J.M.And., sp. nov.

**Holotype**
Specimen: BP/2/1548; pl. 93.
Assemblage: Lit 111 Dic/Hei, Little Switzerland.
Preservation: partial frond, compression in thickly laminated, carbonaceous (cuticle), olive-grey shale with moderate cleavage.

**Reference palaeodeme**
Assemblage (TC): as for holotype.
Specimens: 9 indivs (1 complete, 8 intact to frags), pls 93–96.

**Sister palaeodemes**—4
Pen 321 Dic/Ris: 5% of TC, 42 indivs (intact to frags), pls 97, 98.
Maz 211 Hei/Dic: 3 indivs (3 frags).
Kra 111 Dic odo: 4% of TC, 24 indivs (11 intact, 10 partial, 3 frags).
Aas 411 Dic/Sph: 1 indiv. (frag.).

**Specific diagnosis**
A *Nymboidiantum* species with bipinnate frond bearing entire to lobed alternate broad-elliptic pinnules with contracted acroscopic base and decurrent basiscopic base and one to three decurrent veins entering base of pin-
nule and forking to four times and radiating to apical margin.

**Specific characters**
Sterile foliage: frond bipinnate, of medium size, up to ca 250 mm long;
pinnate up to 50 mm, attached at a high angle in midfrond; pinnules closely spaced, attached at ca 45°, alternate, broad-elliptic, ca 10 mm long by 5 mm wide, with contracted acroscopic base and decurrent basi-
scopic base, margin entire to lobed; venation without midvein, 1 to 3
decurrent veins enter base, forking up to four times, radiating slightly
to the apical margin.

**Eponymy**
*schwyzeri*—after Heidi’s father, the late Rolf Schwyzer, an engineer who, in retirement, studied geology. He assisted us in the collection of fos-
sils from this locality and was always very supportive in all aspects of
our research.

**Comment & comparison**
Some specimens of *N. schwyzeri* from Lit 111 yielded cuticular structure and even at low magnification (× 5) cell structure was evident, pl. 93(4). Two cuticle preparations made in January 1974 showed cell structure. However, further preparations in June 1990 yielded poor results. The former material showed numerous stomata longitudinally aligned between the veins. The arrangement of the subsidiary cells was not clear but they appeared to have numbered more than two. Future studies on the cuticle of *Nymboidiantum* is warranted.

Compared with the five species of *Nymboidiantum* described by Holmes (2003) from Nymboida, Australia, *Nymboidiantum schwyzeri* is closest to *N. glossophyllum* and *N. robustum*. *N. glossophyllum* differs by the more widely spaced pinnules and the often deeply divided lamina of the proximal pinnules, while *N. robustum* differs by the broader pinnule attachment.

One individual from Lit 111, pl. 96(5), and some from Pen 321 are super-
ificially similar to *Nymbiella lacerata* Holmes (2003) from Nymboida in that their pinnules are not constricted at the base and by the parallel lateral veins pro-
ceeding at a high angle to the pinnule distal margin. However, in this Molteno material the lateral veins originate from a single acutely decurrent vein and not directly from the pinna rachis as in *N. lacerata*. The two specimens illus-
trated on pl. 96(3, 4) have more elongated narrow pinnules and are doubtfully included here.
Nymboidiantum schwyzeri

pl. 93

?POLYPODIALES
Nymboidiantum schwyrzi

Little Switzerland
(Lit 111 Dic/Hei)

af PRE/F8563a

POLYPODIALES

pl. 94

Nymboidiantum schwyrzi
Little Switzerland
(Lit 111 DicHei)

at PRE/F/1549
Nymboidiantum schwyzeri

Little Switzerland
(Lit 111 Dic/Hei)

PRE/F/5562a (figs 1, 2)

BP/2/1546

BP/2/2064
Nymboidiantum schwyzeri

Peninsula
(Pen 321 DioRis)
Nymboidiantum schwyzeri

Peninsula
(Pen 321 Dic/Ris)

PRE/F/13592a

PRE/F/13595a

PRE/F/13600

PRE/F/13596

PRE/F/13595'y'b

PRE/F/13595'x'b

PRE/F/13597

PRE/F/13597

?POLYPODIALES

pl. 98

Nymboidiantum schwyzeri
POLYPODIALES A.B. Frank 1877

Displinites H.M. And. & J.M. And., gen. nov.

Type species
Displinites variabilis H.M. And. & J.M. And., sp. nov.
Umkomas Valley, Molteno Fm., Karoo Basin, S. Africa; Carnian, Triassic.

Generic diagnosis
A ?polypodiaceous fern based on sterile dichotomous fronds with a long slender rachis (petiole) bearing a pair of bilobed to deeply segmented pinnae with forking radiating veins but no midrib.

Generic characters
Sterile foliage: frond dichotomous, 20–60 mm long, with slender elongated rachis (petiole); pinnae attached beyond dichotomy, base contracted to strongly petiolate, elliptic to broadly ovate, bilobed to multiply lobed with deeply incised segments with rounded apices; veins enter base of lobes singly, then fork several times, radiating to apical margin.

Etymology
Displinites—contrived, with reference to the dichotomous branching and the laminae with venation similar to that of the extant fern genus Asplenium.

Global range: 1 sp., Gondwana, Tr. (CRN). First & last: the Molteno species described here.

Gondwana Triassic occurrence
Frequency (F): 2 degree squares (of the 84 across Gondwana).
Ubiquity (U): 1 continent (of 5 comprising Gondwana).
Diversity (D): 1 species.
Abundance (A): <1% (the norm in Molteno TCs).
Longevity (L): 2 myrs (lower Carnian).

Colonisation success: FUDAL rating 2/1/1/-2 = 6.
Endemism: Molteno Fm. endemic.

Molteno occurrence
Frequency (F): 2 TCs (of the 100 sampled in the Molteno).
Diversity (D): 1 species.
Abundance (A): 14 indivs total, extremely rare.

Classification & comparison
Intergeneric comparison
Differs from Nymboidiunum, which has similar venation, by the dichotomous rachis and from Walkomiopteris (Holmes & Anderson 2005), which has similar divided pinnae, by the thin rachis, delicate venation and sometimes multiple pinnae.

Comparisons beyond Gondwana Triassic
Extant ferns
The fern genera Adiantum and Asplenium also have pinnules with contracted bases and radiating venation but both have characteristic sori.

Displinites

Displinites variabilis

1. PB/2/533 pl. 99(2, 8)
Holotype

2. PRE/F/414a R2 x 2
pl. 99(1, 7)

3. PRE/F/415 R2 x 2
pl. 99(4, 9)

4. PRE/F/94 R2 x 2
pl. 99(5, 6)

all Umk 111
**Displinites variabilis** H.M.And. & J.M.And., sp. nov.

**Holotype**
*Specimen*: PRE/F/533; pls 99(2, 8), 100(1).
*Assemblage*: Umk 111 Dic 2 spp, Umkomaas Valley.
*Preservation*: ?complete frond, compression in thinly laminated, carbonaceous (cuticle), moderately baked, dark grey shale with good cleavage.

**Reference palaeodeme**
*Assemblage* (TC): as for holotype.
*Specimens*: 13 indivs (5 ?complete, 8 intact), pls 99, 100.

**Sister palaeodemes**
Bir 111 Sph 2 spp: 1 indiv. (intact), BP/2/4713a,b.

**Specific diagnosis**—as for genus.

**Specific characters**—as for genus.

**Etymology**
*variabilis*—referring to the variable shape of the pinnae.

**Comment & comparison**
*Displinites* is close to *Nymboidiantum* in having constricted bases to the pinnules and with similar venation, but the overall morphology of the frond with the forking rachis is distinct. The dichotomous rachis bearing a pair of double-lobed pinnae of *Walkomiopteris eskensis* (Walkom) Holmes & Anderson (2005) is similar to *Displinites variabilis*. However, *D. variabilis* is differentiated by the slender rachis and sometimes multiple pinnae with more delicate venation.
Displinites variabilis

Pl. 99

Polypodiales
Displinites variabilis

Umkomaas Valley
(Umk 111 Dic 2iipp)
**Molteniella** H.M. And. & J.M. And., gen. nov.

### Type species

*Molteniella terblanchiorum* H.M. And. & J.M. And., sp. nov.

Aas 411 Dict/Sph, Aasvoëlberg, Molteno Fm., Karoo Basin, S. Africa; Carnian, Triassic.

### Generic diagnosis

A ?polypodialean fern based on sterile ?bipinnate very small fronds bearing small lanceolate pinnules with a midvein and ca 10 pairs of lateral veins.

### Generic characteristics

**Sterile foliage:** fronds probably bipinnate, *ca* 75 mm long as preserved; pinnae *ca* 30 mm long bearing more than 15 pairs of pinnules; pinnules small, *ca* 2–6 mm long and *ca* 1 mm wide, lanceolate, apex acute; venation with prominent midvein and ca 10 pairs of fine once-forking lateral veins.

### Etymology

*Molteniella*—contrived name from Molteno and the diminutive size of the frond.

### Global range

1 sp., Gondwana, Tr.(CRN).

First & last: the Molteno species described here.

### Gondwana Triassic occurrence

**Habit:** possibly an epiphyte (most extant Hymenophyllaceae, i.e. filmy ferns, occur as epiphytes in mossy forests).

**Preferred habitat:** Sphenobaiera woodland.

### Classification & comparison

**Intergeneric comparison**

*Molteniella* could also be interpreted as a pinnate fern if the axis is taken to be a rhizome, which is how Holmes (2003) interpreted the thick axis of his genus *Micronymbopteris*. Regardless of the interpretation, the ultimate leaflets (i.e. pinnules or pinnae) of *Micronymbopteris* differ from *Molteniella* by their shorter length, rounded apex and thick texture.

**Comparisons beyond Gondwana Triassic**

*Lausarian Triassic*

Recently Axsmith et al. (2001) described the first definitive fertile filmy fern from the Late Triassic of North Carolina, USA, as *Hopetedia praetermissa*.

This is similar to the Molteno fern but the pinnules have only a single vein and are fertile.

The North Carolina species has pushed back the fossil record of the Hymenophyllaceae from the Late Cretaceous (Skog 2001) to the Late Triassic. Thus it may not be unexpected to find filmy ferns in the Molteno Fm.

**Extant ferns**

The filmy ferns in the family Hymenophyllaceae have a frond morphology of three orders of segments with the ultimate order distinctly lobed and with very thin membranaceous laminae. Similar features occur in *Molteniella*, but as there is no fertile material available its classification remains uncertain.
Drepanozamites dutoitii

Holotype

Hlatimbe Valley
(Hla 213 Dic eto)

MARATTIALES
Hlatimbe Valley
(Hla 213 Dic elo)
**Asterotheca chevronervia**

**pl. 103**

**MARATTIALES**
Asterotheca chevronervia

all PRE/F:20365a

Konings Kroon
(Kon 223 Dic odo)
Konings Kroon
(Kon 223 Dic odo)

all PRE/P/20362a
Konings Kroon
(Kon 223 Dic odo)

Asterotheca chevronervia

MARATTIALES

pl. 106

Asterotheca chevronervia
Asterotheca dewinteri

pl. 107

MARATTIALES

Hlatimbe Valley
(Hla 213 Dic eto)
Hlatimbe Valley
(Hla 213 Dic elo)

Asterotheca dewinteri

MARATTIALES

pl. 108

Asterotheca dewinteri
Umkomaas Valley
(Umk 111 Dic 2spp)

*Asterotheca killickii*

holotype all PRE/F400a

*Pl. 109*
Umkomaas Valley
(Umk 111 Dic 2spp)

Asterotheca killickii

MARATTIALES pl. 110
Konings Kroon
(Kon 211 Ast 2sp)

Osmundopsis sp. cf. O. scalaris

pl. 111

OSMUNDALES
OSMUNDALES

pl. 112

Osmundopsis sp. cf. O. scalaris

Konings Kroon
(Kon 211 Ast 2 spp)
Osmundopsis botryoides

Peninsula
(Pen 311 Hei elo)

Holotype
PRE/F/16892a
Peninsula
(Pen 311 Hei elo)

OSMUNDALES

Osmundopsis botryoides

pl. 114
Peninsula
(Pen 311 Hei elo)

all PRE/F/16892a,b
Holotype

Osmundopsis botryoides
pl. 115
Osmundopsis petiolaris

Umkomaas Valley
(Umk 111 Dic 2ssp)

all PRE/F:405a,b
Holotype
Osmundopsis racemosus

pl. 117

OSMUNDALES

Aasvoëlberg
(Aas 411 Dio/Sph)
Aasvoëlberg
(Aas 411 Dio/Sph)

all PRE/F/21842a
Holotype
Rooitodites pulchra

Holotype

Konings Kroon
(Kun 211 Ast 2 spp)

OSMUNDALES
all BP/2/4211b/z
Holotype

Konings Kroon
(Kon 211 Ast 2app)
Rooitodites integra (Kan 11 Ast spA)

Kannaskop

PRE/F/13362a x 2.5
PRE/F/13365 x 10
PRE/F/13362a x 10
Kannaskop
(Kan 111 Åst spA)

af PRE/F/13355a
Holotype
Birtodites holmesii

Birds River
(Bir 111 Sph 2pp)
Birds River
(Bir 111 Sph 2 spp)

all PRE/F/10709a
Holotype
Birds River
(Bir 111 Sph 2spp)

Birtodites holmesii

all PRE/F10709a
Holotype
Birds River
(Bir 111 Sph 2 spp)
Aasvoëlberg
(Aas 411 Dic/Sph)

al PRE/F/20743

Birtodites holmesii
pl. 127
OSMUNDALES
Birtodites holmesii

Aasvoëlbberg
(Aas 411 Dic/Sph)

figs 1–3, all PRE/F/12086

figs 4–6, all PRE/F/12038a
Elantodites turneri

Elandspruit
(Ela 112 Equ sp)

Holotype

all PRE/F/13240a

228 S T R E L I T Z I A 21 (2008)
Elantodites turneri

Elandspruit

(Ela 112 Equ sp)

Holotype

PRE/F/13240a

OSMUNDALES

pl. 130

Elantodites turneri
Elantodites turneri
pl. 131

Elandspruit
(Ela 112 Équ sp)

all PRE/F/13239
Elandspruit
(Ela 112 Equ sp)

Elantodites turneri
pl. 132

all PRE/F13246
Elantodites turneri

Peninsula (Pen 222 Dic/Equ)

all PRE/F/14078b

OSMUNDALES
Elantodites turneri

Peninsula
(Pen 222 Dio/Eq)

all PRE/F/14067
Telemachus Spruit
(Tel 111 Hei elo)

el PRE/F/18290b

Elantodites turneri

pl. 135

OSMUNDALES
Telemachus Spruit
(Tel 111 Hei elo)

Elantodites turneri
Elantodites turneri

pl. 137

OSMUNDALES

Aasvoëlberg
(Aas 111 Hei elo)

all PRE/F/19490a
(two small fertile fragments occur in close proximity on the same slab)
Birds River
(Bir 111 Sph 2 spp)
all BP/24709
Holotype

Elantodites stuartii
pl. 139
OSMUNDALES
Birds River
(Bir 111 Sph 2 spp)

Elantodites stuartii
Elantodites alisoniae

pl. 141

OSMUNDALES

Birds River
(Bir 111 Sph 2app)

af BP/2/4739a
Holotype
Birds River
(Bir 111 Sph 2spp)

at BP/2/4739a
Birds River
(Bir 111 Sph 2 spp)

at BP/2/4739a

Elantodites alisoniae

pl. 143

OSMUNDALES
Elantodites kitchingii

Konings Kroon (Kon 211 Ast 2app)

Holotype

pl. 145

OSMUNDALES
Elantspruit
(Ela 112 Equ sp)
all PRE/F/13222a

Elantodites kitchingii
pl. 147
OSMUNDALES
Elantodites kitchingii

pl. 148
Elantodites kitchingii

Pl. 149

Elandspruit
(El 112 Equ sp)
Elantspruit
(Ela 112 Equ sp)

Elantodites kitchingii

all PRE/F/13233a

OSMUNDALES

Elantodites kitchingii

pl. 150
Dictyophyllum bremerense

pl. 151

POLYPODIALES
Telemachus Spruit
(Tel 111 Hei elo)
ictyophyllum bremerense

PRE/F/17481 (figs 1–3)

Lutherskop
(Lut 311 Hei elo)
ictyophyllum ellenbergi

PRE/F/11112b

OSMUNDALES
pl. 152

Dictyophyllum
BIBLIOGRAPHY, GLOSSARY & INDEX
BIBLIOGRAPHY


**GLOSSARY**

Here we include only a few terms and concepts that are used widely in this volume on the Molteno ferns. For a fuller glossary see our ‘Heyday of the Gymnosperms’ (And. & And. 2003). Usage is as introduced or used in our Molteno series.

**SAMPLING**

*Frequency:* The measure of frequency of a fossil taxon within a formation is the number of taphocoenoses (TCs) or assemblages, out of the total sampled, in which it has been found. Through the Gondwana Triassic, for instance, it might be the number of degree squares (out of the total sampled) in which it has been found.

*Abundance:* The abundance of a fossil taxon is a measure of the absolute or relative number of individuals collected from or encountered in an assemblage, formation, region or continent.

*Assemblage:* The full suite of fossil individuals or palaeodemes collected from a distinct lithological unit (lithosome) of limited geographic and stratigraphic extent. A megaplant assemblage will generally represent a localised mosaic of plant associations, less often a single association, through several generations.

*Locality:* An area to about 1 km in diameter, which may include continuous fossiliferous exposure, but will generally include one or more productive exposures of lesser rank.

*Taphocoenosis* (TC): Taphonomic assemblage; fossil assemblage resulting from the taphonomic process; the aggregate of fossil remains contained in a deposit or bed.

**PALAEODEMES**

*Palaeodeme* (fossil population): A collection of fossil specimens judged to represent a single potentially interbreeding population of plants or animals, showing a normal distribution of variation for selected diagnostic characters, and derived from a single taphocoenosis from a discrete small-scale lithological unit (lithosome) such as an abandoned channel infill or crevasse splay.

*Reference palaeodeme* (RP): The most comprehensive, representative, photographically documented palaeodeme in the literature proposed as reference for a particular infrageneric taxon.

*Sister palaeodeme:* A palaeodeme belonging to the same species (in this volume, from the same formation, i.e. the Molteno).

**OCCURRENCE**


In the Molteno Fm., for instance, *Dicroidium*, with a FUDAL rating of 188, was clearly the most successful plant genus, as it was throughout the Gondwana Triassic.
INDEX TO CURRENT MOLTENO ORDERS, FAMILIES, GENERA AND SPECIES

This index leads the reader only to the main treatments of the orders, families, genera and species.

Asterotheca ................................................. 38
  chevroneria ........................................... 40
dewinteri .................................................. 41
killickii .................................................... 44

ASTEROTHECACEAE ....................................... 38

Birmoltia ................................................... 166
  intervenatus ............................................... 166

Birtodites .................................................. 72
  holmesii ............................................... 74

Cladophlebis ............................................. 130
  barbara .................................................. 134
evelynae .................................................. 135
felixii ...................................................... 135
janetiae .................................................... 134
katherineae ............................................... 133
moltenensis .............................................. 133
paucinerva ............................................... 132
rozenaria .................................................. 132

Dictyophyllum ........................................... 122
  bremerense ............................................. 124
enellenbergii .......................................... 123
shirleyi ................................................... 125

DIPTERIDACEAE .......................................... 122

Displinites ................................................ 192
  variabilis .............................................. 193

Drepanozamites ........................................ 32
dutoitii .................................................... 34
harrisii ................................................... 35

Elantodites ............................................... 82
  alisoniae .............................................. 92
  joydentiorum .................................. 96

kitchingii ............................................... 94
nwartii .................................................. 90
turneri ................................................... 86

MARATTIALES ............................................ 32

Molteniella .............................................. 196
terblanchiorum ...................................... 197

Nymboidiantum .......................................... 184

Nymbopteran ............................................ 170

Osmundopsis .............................................. 171

OSMUNDACEAE ............................................ 46, 52, 72, 82

Osmundales .............................................. 122

Parsorophyllum ......................................... 174
  africana .................................................. 175

POLYPODIALES .......................................... 184, 192, 196

Rootodites ................................................ 52

Sphenopteris ............................................ 162
  annakatae ............................................ 162

Stormbergia ............................................ 181
  gardneri ............................................... 182
  rosiae .................................................. 182

TRELIIZIA 21 (2008)
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SYSTEMATICS OF THE MOLTENO FERNS
**MARATTIALES** Prantl 1874

**MARATTIACEAE** Brecht. & J. Presl 1820

**Drepanozamites** Harris 1932

**Type species**

*Drepanozamites nilssonii* Harris 1932

Astart River Bed A, Scoresby Sound, E. Greenland; Rhaetic, Triassic.

**Generic concept**

A marattiaceous pinnate frond bearing sickle-shaped pinnae with veins forking and diverging up to 6 times, and with ovoid sporangia closely aligned along the acroscopic margin.

**Generic characters**

**Fertile foliage:**

- **frond** pinnate; **pinnae** sickle-shaped, constricted at base; **veins** enter each pinna singly then diverge and fork up to 6 times to end along acroscopic margin; **sporangia** ovoid, closely aligned on veins along acroscopic margin.

**Sterile foliage:**

- frond similar to above; **pinnae** markedly larger; **veins** more numerous, closely spaced, diverging and forking up to 6 times, ending mainly along acroscopic but also on basiscopic margin.

**Etymology**

*Drepanozamites*—*drepan* (Gr.) for sickle, after the falcate shape of the pinnae; *Zamites* a cycad genus.

**Global range:** 3 spp, Pangaea, Tr. (CRN–RHA).

**First:** the Molteno species described here.

**Last:** *Drepanozamites nilssonii* (Harris 1932); Scoresby Sound, E. Greenland.

**Gondwana Triassic occurrence**

- **Frequency (F):** 1 degree square (of the 84 across Gondwana).
- **Ubiquity (U):** 1 continent (of 5 comprising Gondwana).
- **Diversity (D):** 2 species.
- **Abundance (A):** <1% (the norm in Molteno TCs).
- **Longevity (L):** 1 myrs (lower Carnian).
- **Colonisation success:** FUDAL rating 1/1/2/-/1 = 5.
- **Endemism:** single basin endemic.

**Molteno occurrence**

- **Frequency (F):** 3 TCs (of 100 sampled in the Molteno).
- **Diversity (D):** 2 species.
- **Abundance (A):** 22 indivs total, very rare.

- **Habit:** possibly a small epiphytic fern.
- **Preferred habitat:** *Dicroidium* riparian forest (type 1, mature).

**Affiliation**

(fertile & sterile fronds)

Though the available Molteno material is sparse, it is clearly preserved, and affiliation between fertile and sterile fronds at generic level appears well established. The affiliation at species level is less sure (see notes for *D. dutoitii* under comments and comparisons).

**Classification & comparison**

**Suprageneric classification**

Marattiaceae/Marattiales

Harris (1932), when he found that the cuticle was not allied to the cycads or the Bennettitales, placed *Drepanozamites* in Seed Plant Incertae Sedis. The discovery of fertile fronds in the Molteno, with large ovoid bodies assumed to be sporangia aligned along the acroscopic margin shows the genus to be a fern most probably in the order Marattiales and family Marattiaceae. As the detailed structure of the ovoid bodies is as yet unknown and no extant members of the Marattiaceae have sickle-shaped pinnae, this classification needs confirmation.

**Intergeneric comparison**

Harris (1932) noted that *Drepanozamites* resembled *Otozamites* and to a lesser extent *Sphenozamites* and *Plagiozamites* in general form and venation, but that the cuticle structure was quite distinct. Nathorst (1878) originally placed *Drepanozamites nilssonii* (Harris 1932) from Sweden in the fern genus *Adiantites*. In the Molteno, the genera *Nymboidiantum* and *Displinites* also have constricted pinnales but are not sickle-shaped.

**Interspecific comparison**

*Drepanozamites nilssonii* from Greenland is close to the specimens of *D. harrisii* from the Molteno but the pinnae are twice as large. Both these species are known only from sterile fronds, while *D. dutoitii* is based on fertile fronds.
and an affiliated sterile pinna. *D. nilssonii*, as described by Harris (1932), has a thin cuticle with simple unspecialised stomata on the lower surface and thick-ened cells (hair bases) along the veins. No cuticular structures were obtained from the Molteno material although four peels were taken from Umk 111 and macerated.

**Comparisons beyond Gondwana Triassic**

**Gondwana Permian**

Liknopetalon from the Late Permian of South Africa (And. & And. 1985; Adendorff et al. 2003) has a similar arrangement of fertile ovoid bodies (also of unknown structure). However, the pinnae are fan-shaped and the dichotomous veins are reported as having a few anastomoses.

**Extant ferns**

In the Polypodiales, the extant genus *Adiantum* has similar sickle-shaped pinnae in a number of species, e.g. *A. incisum*, that occur in tropical and subtropical Africa. The pseudo-indusia and sori along the acroscopic margins of this fern are superficially similar to the ovoid structures on the fertile *Drepanozamites* frond from the Molteno.

**Rarity & quality of fertile Molteno material** (Tab. 12)

Of the two Molteno species of this genus, *D. harrisii* is represented by 19 indivs from 2 TCs, but has no fertile material; whilst *D. dutoitii* is known from just 3 indivs from 1 TC and two of these are fertile. The holotype (PRE/F/8669; pls 101, 102) is by far the better preserved of these two specimens; the second specimen adds no further diagnostic details.

---

**Tab. 12. Drepanozamites, Molteno occurrence**

<table>
<thead>
<tr>
<th>assemblages (taphocoenoses)</th>
<th></th>
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</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>f</td>
<td>s</td>
<td>f</td>
<td>s</td>
<td></td>
</tr>
<tr>
<td>Hla 212 Dic 3 spp</td>
<td>-</td>
<td>-</td>
<td>1</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Hla 213 Dic elb</td>
<td>2</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Umk 111 Dic 2 spp</td>
<td>-</td>
<td>18</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total TCs</td>
<td>1</td>
<td>2</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total indivs</td>
<td>2</td>
<td>19</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Drepanozamites dutoitii  
H.M.And. & J.M.And., sp. nov.

Holotype
Specimen: PRE/F/8669a,b; pls 101, 102.
Assemblage: Hla 213 Dic 3spp, Hatimbe Valley.
Preservation: fairly complete fertile leaf, with counterpart; compression in thinly laminated, carbonaceous (poor cuticle), medium dark grey shale with good cleavage.

Reference palaeodeme
Assemblage (TC): as for holotype.
Specimens: 2 fertile indivs, (1 ca complete, 1 intact), pls 101, 102(1, 3–5).
1 sterile indiv. (1 pinnule), pl. 102(2).

Sister palaeodemes—nil.

Specific diagnosis
A Drepanozamites species with fertile fronds bearing ovoid sporangia and sterile fronds with pinnae to ca 20 mm long and distinctly asymmetrically lobed at the distal margin.

Specific characters
Fertile foliage: frond pinnate, ca 80 mm long; pinnae sickle-shaped, ca 7 × 3 mm; veins diverging and forking up to 6 times, with ca 23 veins ending at the acroscopic margin; sporangia up to ca 16, ovoid, ca 0.6 mm long, closely aligned on veins along acroscopic margin.
Sterile foliage: frond unknown; pinnae sickle-shaped, ca 23 × 7 mm, apical margin distinctly asymmetrically bilobed; venation diverging and forking up to 6 times, with numerous veins ending at the acroscopic, apical and distal half of the basiscopic margins.

Eponymy
dutoitii—after Dr Alex Du Toit, the eminent South African geologist who published the first review of the Molteno flora in 1927.

Comment & comparison
This species, represented by two intact (one fairly complete, one fragmentary) fertile fronds and a single detached sterile pinnule from Hla 213, appears to be clearly distinct from both D. nilssonii from Greenland and D. harrisii from the Molteno (Umk 111). The true nature of this distinctiveness, however, depends on the validity of the affiliation (not certain) of the fertile and sterile foliage.

Though the fertile pinnae of D. dutoitii are only around half the size of the sterile pinnae of D. harrisii, the single large sterile pinna of the former is distinctive in its marked distal lobing. The fertile pinnae are very different from their putative sterile affiliates in their smaller size, in the venation being more widely spaced, and in the absence of any veins terminating along the basiscopic margin.

The sterile pinna (tf 3) is drawn from the × 20 magnification of the holotype, pl. 102(3), and shows ca 16 sporangia. The form of the sporangial opening adjacent to the margin is not clear, but appears to be comprised of a broad band of specialised cells (tf 4).
Drepanozamites harrisii H.M. And. & J.M. And., sp. nov.

Holotype
Specimen: BP/2/529a,b; pls 1(1, 2), 2(1, 6)
Assemblage: Umk 111 Dic 2spp, Umkomaas Valley.
Preservation: complete frond, compression in thinly laminated, carbonaceous (cuticle), moderately baked, dark grey shale with good cleavage.

Reference palaeodeme
Assemblage (TC): as for holotype.
Specimens: 18 indiv sterile (1 complete, 7 intact, 10 isolated pinnae), pls 1, 2.

Specific diagnosis
A Drepanozamites species based only on sterile fronds with pinnae up to 20 mm long and showing barely incipient asymmetrical lobes at distal margin.

Specific characters
Fertile foliage: unknown
Sterile foliage: frond pinnate, ca 150 mm long; pinnae sickle-shaped, to ca 20 × 6 mm; venation diverging and forking up to 6 times, with ca 45–50 veins ending along the acroscopic, apical and distal half of the basiscopic margins.

Eponymy
harrisii—after Prof. T.M. Harris, the renowned palaeobotanist who worked on the Greenland and Yorkshire fossil floras and was mentor to one of us (HMA) at Reading University in 1968.

Comment & comparison
See under D. dutoitii and interspecific comparisons under genus.
Drepanozamites harrisii

pl. 1

MARATTIALES
MARATTIALES

pl. 2

Drepanozamites harrisii

Umkomaas Valley
(Umk 111 Dic 2spp)
MARATTIALES Prantl 1874

ASTEROTHECACEAE Sze Xingjian & Li Xingxue 1963

*Asterotheca* Presl in Corda 1845

Type species
Asterotheca sternbergii Goeppert (1836, pl. 6, figs 1–4): Carboniferous.

See *Asterotheca sternbergii* (Goeppert) Presl in Corda 1845.

**Generic concept**
A marattialean fern with pecopteroid pinnules bearing adjacent synangia occurring between midvein and margin and composed of groups of sporangia conjoined at base and dehiscing along an apical suture line.

**Generic characters**
Fertile foliage: frond pinnate to ?tripinnate, up to an estimated 2 m long; venation pecopteroid; synangia adjacent, occurring between midvein and margin, composed of groups of sporangia conjoined at base; sporangia dehiscing along an apical suture line and without an annulus.

Sterile foliage: similar to fertile foliage; venation pecopteroid, midrib distintinct, lateral veins mainly unforked or forking once.

**Etymology**
*Asterotheca*—referring to the star-like form of the synangia.

**Global range:** numerous spp, Pangaea, C.–Late J.

**Gondwana Triassic occurrence**
Frequency (F): 15 degree squares (of the 84 across Gondwana).
Ubiquity (U): 3 continents (of 5 comprising Gondwana).
Diversity (D): 12 species.
Abundance (A): 1% (the norm in Molteno TCs).
Coloniisation success: FUDAL rating 15/3/12/1%/23 = 54.
Endemism: disjunct between Eastern and Western Gondwana.

**Molteno occurrence**
Frequency (F): 6 TCs (of 100 sampled in the Molteno).
Diversity (D): 3 species.
Abundance (A): 43 indivs total, very rare to extremely rare.

Habit: some are possibly tree ferns with fronds to 2 m.
Preferred habitat: from riparian forest to woodland.

Affiliation (fertile & sterile fronds)
Holmes (2001, figs 12A–C) illustrated *Asterotheca chevronervia* from Nymboida, Australia, with fertile and sterile pinnules on the same frond. In the Molteno, both fertile and sterile pinnules occur on the same pinnae in specimens from Kon 223, pls 103(1, 2), 106(3, 4) and Kon 222. For the other two Molteno species (*A. dewinteri* and *A. killickii*), sterile fronds have been affiliated based on mutual occurrence at Hla 213 and Hla 211 respectively.

**Classification & comparison**
Suprageneric classification (*Asterothecaceae/Marattiales*)
Andrews et al. (1970) placed *Asterotheca* in the Marattiales. The genus includes numerous fertile species from the Carboniferous to the Jurassic. As details of sporangial structure become known it will probably be divided into a number of separate genera. Similar ferns known only from sterile material are often placed in the genus *Pecopteris* (Andrews et al. 1970).

Intergeneric comparison
*Eboracia herbstii*, a Triassic fossil fern from Australia (Playford et al. 1982), was identified on the basally expanded pinnules and not on the form of the 5–8 sporangia on each pinnule. On the basis of the fertile material we question the placement of this fossil in *Eboracia*. The type species, *E. lobifolia* (Harris 1961), has ‘sori 1–4 on each margin, always strongly recurved’ and this is quite unlike *E. herbstii* that has sori/synangia akin to *Asterotheca*. This specimen is thus transferred to *Asterotheca herbstii* (Rigby 1982), comb. nov.

The genus *Gleichenites* has been used for South American Triassic material (Herbst 1972, 1996). Holmes (2001) followed Herbst (1974) and used the genus for Australian Nymboida material. However, none of these fossils have well-preserved sporangia or the typical forking fronds to confirm this identification. With better-preserved material they may prove to belong in *Asterotheca* or other genera rather than *Gleichenites*.

**Interspecific comparison**
Of the numerous species described from the Gondwana Triassic, 13 are here recognised as valid species (Tab. 4), and see Hypodigm (Tab. 11).
Argentinian and Australian species were compared by Herbst (1977a) and Holmes (2001).

**Gondwana occurrence** (elaborated)

*Gondwana Triassic (South Africa).*

One species of *Asterotheca* was recorded from the Burgersdorp Fm. (And. & And. 1985).

*Gondwana Permian* (South Africa).

Two species of *Asterotheca* were recorded from the Vryheid Fm. (And. & And. 1985).

**Laurasian occurrences** (elaborated)

In the Santa Clara flora from the Late Triassic of Mexico, *Asterotheca santaclarae* (Webber 1985a) is the most common fern. It is somewhat similar to the Molteno species *A. dewinteri*.

**Rarity & quality of the Molteno fertile material** (Tab.13)

Though not quite as infrequent and rare as for *Osmundopsis*, fertile specimens of *Asterotheca* are nevertheless extremely rare. Of the 3 species, one (*A. dewinteri*) occurs in just one TC, the second (*A. killickii*) in 2 TCs, and the third (*A. chevronervia*) in 3 TCs—in all cases particularly rarely. Only one specimen of each species (as for *Osmundopsis*) reveals the basic morphology of the synangia or sporangia.

*A. chevronervia* (Kon 223, pls 103–106): of the 5 fertile indivs from the RP only the one (PRE/F/20365a,b; pls 103, 104) shows the general structure of the synangia with its four conjoined sporangia. The 2 fertile indivs from the SP (Kon 222) show no such details.

*A. dewinteri* (Hla 213, pls 107, 108): all 3 available fertile indivs are shown in the colour plates. Only the holotype (PRE/F/1170a), on two adjacent pinnules, shows the nature of the synangia with four conjoined sporangia.

*A. killickii* (Umk 111, pls 109, 110): of the 9 fertile indivs from the RP (Umk 111) and the 2 fertile indivs from the single SP (Hla 211), just the holotype (PRE/F/400a, b), from the former, shows the clear seed-like morphology of the synangium. As noted elsewhere, it might well be that this species will prove to be a gymnosperm rather than a fern.

**Gondwana Triassic, ‘GEOSTRAT’ DISTRIBUTION**

![Gondwana Triassic map](image)

---

**Tab. 13. *Asterotheca*, Molteno occurrence**

<table>
<thead>
<tr>
<th></th>
<th>A. chevronervia (Kon 223)</th>
<th>A. dewinteri (Hla 213)</th>
<th>A. killickii</th>
</tr>
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<tbody>
<tr>
<td></td>
<td>f</td>
<td>s</td>
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<tr>
<td>Kon 223</td>
<td>5</td>
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<tr>
<td>Kon 222</td>
<td>2</td>
<td>1</td>
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</tr>
<tr>
<td>Hla 211</td>
<td>-</td>
<td>-</td>
<td>-</td>
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<tr>
<td>Hla 213</td>
<td>-</td>
<td>3</td>
<td>1</td>
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<td>Umk 111</td>
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<td>Aas 411</td>
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<tr>
<td>Total TCs</td>
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<td>1</td>
</tr>
<tr>
<td>Total indivs</td>
<td>9</td>
<td>2</td>
<td>3</td>
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</table>
**Asterotheca chevronervia** Holmes 2001

**Holotype**

*Specimen:* AMF 113414, Australian Museum, Sydney.

*Assemblage:* Reserve Quarry, Nymboida, Basin Creek Fm., Nymboida C.M., Australia; Ladinian, M. Triassic.

*Preservation:* an intact frond, no cuticle preserved, fine siltstone, poorly bedded.

**Reference palaeodeme**

*Assemblage* (TC): as for holotype.

*Specimens:* 8 indivs mentioned (some intact), Holmes 2001, pls 11A, 12A–D.

**Sister palaeodemes—3**

Kon 223 Dicodo: 1% of TC, 8 indivs (5 fertile, partial; 3 sterile, 1 intact, 2 partial), pls 3(1, 2), 103–106.

Kon 222 Dicodo: 1% of TC, 19 indivs (2 fertile, partial; 17 sterile, partial), pls 3(3–6), 4.

Aas 411 Dic/Sph: 2 indivs (2 fertile, frags).

**Specific concept**

An *Asterotheca* species with fertile pinnules bearing relatively small (ca 0.5 mm diam.) roundly cubic synangia with cross-axes at ca 90º to midrib.

**Specific characters**

**Fertile foliage:** *frond* large, bipinnate to ?tripinnate; *pinnae* closely spaced, subopposite to alternate, ca 80 × 10 mm, L:W ratio 8:1; *pinnules* ca 6 × 1.5 mm, bearing 8–12 pairs of synangia that almost fill the lamina surface between midvein and margin; *synangia* (based on Kon 223) in single rows down either side of midrib, ca 0.5 mm diam., spherical to roundly cubic, consisting of 4 conjoined sporangia, cross-axes dividing synangium at ca 90 degrees to midrib; *sporangia* details unknown.

**Sterile foliage:** *frond* up to 2 m long, bipinnate to ?tripinnate; *pinnae* closely spaced, subopposite to alternate, up to ca 120 × 10 mm, L:W ratio 8–12:1; *pinnules* pecopteroid, closely spaced to overlapping, ca 3–6 × 1–2 mm, L:W ratio 2.5–3:1; *lateral veins* in ca 10 pairs, mainly unforked, departing from midvein at ca 45º–60º and run straight to margin.

**Etymology**

*chevronervia*—with reference to the chevron-like arrangement of the lateral veins.

**Comment & comparison**

This species, represented by the three palaeodemes, is distinguished from the other *Asterotheca* species in the Molteno by the mainly unforked lateral veins, smaller size and lesser length to width ratio. It is the dominant fern at both the Kon 222 and Kon 223 TCs, while at Aas 411 only two individuals are known in an assemblage that includes nine fern taxa. Occasional forking veins are evident, pl. 4(1, 3). Complete fronds have not been found, but it is certainly bipinnate as indicated by the alignment of pinnae as shown on pl. 3(3). Holmes (2001) suggested that the bipinnate fronds would have been up to 2 m long and based on associated axes (up to 40 mm wide) that it may even be tripinnate and have exceeded 3 m.

In the Molteno this species has previously been described as *Cladophlebis nebbensis* by Du Toit (1927) and was figured by us as *Cladophlebus* sp. ‘D’ (And. & And. 1983, pl. 8). The other similar Gondwana Triassic *Asterotheca* species, e.g. *A. hillae*, *A. rigbyana*, and *A. truempyi*, have been discussed and compared by Holmes (2001).

Similar interveinal striae as occur in at least some of the Molteno *A. chevronervia* (e.g. tf.1) material are found in *Birmoltia intervenatus* (Bir111 RP), which suggests that these species could be the fertile and infertile representatives of some supra-specific taxon. The two entities are clearly different at species level: where *A. chevronervia* veins are mainly unforked, those of *B. intervenatus* are mostly once- or twice-forked. It might be noted that Kon 222 is the only TC that includes both species.
**Asterotheca dewinteri** H.M. And. & J.M. And, sp. nov.

**Holotype**
Specimen: PRE/F/1170a, b; pls 107(1–3), 108(1).

**Assemblage**: Hla 213 Dic Jopp, Hlatimbe Valley.

**Preservation**: virtually complete pinna, with counterpart; compression in thinly laminated, carbonaceous (poor cuticle) medium dark grey shale with good cleavage.

**Reference palaeodeme**
Assemblage (TC): as for holotype.
Specimens: 3 fertile indivs (all intact pinnae); 1 sterile pinna (frag.); pls 107, 108.

**Sister palaeodemes**—nil.

**Specific diagnosis**
An *Asterotheca* species with fertile pinnules bearing relatively large (ca 1 mm diam.) spherical synangia with cross-axes at ca 45° to midrib.

**Specific characters**
**Fertile foliage**: frond unknown; *pinnae* uncertain; *pinnules* bearing 9–12 pairs of synangia that almost fill the lamina surface between midvein and margin; *synangia* in single rows down either side of midrib, ca 1 mm diam., spherical, consisting of four conjoined sporangia, cross-axes dividing synangium at ca 45° to midrib; *sporangia* details unknown.

**Sterile foliage**: *frond* and *pinnae* unknown; *pinnule* L:W ratio 4:1; *lateral veins* in ca 12 pairs, fork close to and depart from midvein at ca 45° angle and run straight to margin.

**Eponymy**
dewinteri—after Dr Bernard de Winter, Director of BRI (now SANBI), Pretoria, from 1973 to 1989, who initiated the palaeoflora project.

**Comment & comparison**
The incomplete specimens attributed to this species are assumed to be portions of pinnae of a bipinnate frond.

This species is distinguished from *A. chevronervia* by the larger spherical synangia, the larger pinnules and their greater length:width ratio and by the lateral veins which fork close to the midvein. Other Gondwana Triassic *Asterotheca* species that are closely similar are listed below with their main differences:

- **A. nymboidensis**—contiguous synangia with square outline, occupying all the lamina space, and pinnule L:W ratio of 3–3.5:1.
- **A. menendezii**—contiguous synangia, occupying all the lamina space, and pinnule L:W ratio of 5–5.5:1.
- **A. falcata**—contiguous synangia, with some space along midrib and margin, and pinnule L:W ratio of 4–5.5:1.
- **A. fuchsii**—as described by Townrow (1957) is based on a confusing array of fertile and sterile specimens that defy comparison.

**A. dewinteri** is the only fertile fern known from Hla 213 and is associated with 4 forms of sterile fronds. One fragment (PRE/F/8684), with a distinct midvein and unforked lateral veins, matches the fertile material of *A. dewinteri* and so has been affiliated with this species. A second form (10 indivs) with no clear midvein and simuous forking lateral veins belongs to *Cladophlebis paucinervis*. The remaining five specimens (e.g. PRE/F/8673a, b) with double-forking lateral veins are identified as *C. katherineae*. 

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**MARATTIALES**

**A. dewinteri**

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**PRE/F/1170a**

**pl. 107(2)**

**Holotype**

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**PRE/F/8684**

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**Hla 213**
MARATTIALES

Asterotheca chevroneria

Konings Kroon (Kon 222 Dic odo)

all x 5
**Asterotheca killickii** H.M.And. & J.M.And., sp. nov.

**Holotype**
*Specimen:* PRE/F/400a,b; pls 5(1, 2), 109.
*Assemblage:* Umk 111 Dic 2 spp, Umkomaas Valley.
*Preservation:* an incomplete pinna, with counterpart; compression in thinly laminated, carbonaceous (cuticle), medium dark grey shale with good cleavage.

**Reference palaeodeme**
*Assemblage* (TC): as for holotype.
*Specimens:* 9 indivs fertile (partial); pls 5, 109, 110.

**Sister palaeodemess—**
Hla 211 Dic 3 spp: 2 indivs fertile (partial), 6 indivs sterile (all partial).

**Specific diagnosis**
An *Asterotheca* species with fertile pinnules bearing well-separated pinnules with 4–6 pairs of prominent, protruding, undivided, ovoid ?synangia.

**Specific characters**
*Fertile foliage:* frond unknown; pinnae uncertain; pinnules with L:W ratio 4:1, bearing 4–6 pairs of ?synangia that fill the lamina surface; ?synangia prominent, protruding, undivided, ovoid, ca 0.8 × 1 mm, consisting of a single large sporangium; sporangia details unknown.

*Sterile foliage:* unknown.

**Etymology**
*killickii*—after Dr Donald Killick, Deputy Director of BRI (now SANBI), Pretoria, from 1973 to 1989, our mentor in botanical nomenclature.

**Comment & comparison**
This is a very enigmatic species and with its seed-like ?synangia might prove to be a gymnosperm rather than a fern.

The incomplete specimens attributed to this species are assumed to be portions of pinnae of a bipinnate frond.

*A. killickii* is distinguished from the other *Asterotheca* species by the well-separated pinnules and by the very large protruding ?synangia. It is possible that these ?synangia are composed of a few tightly conjoined sporangia, but more likely that single sporangia (or seeds) are represented. Either way, the protruding form of the bodies, pl. 109(2, 3), is quite unlike the obvious synangia of other *Asterotheca* species.

The two fertile specimens from Hla 211 are best placed in this species although the pinnules are longer and the preservation of the ?synangia is not clear. The 6 sterile fronds are probably affiliated as they compare closely in their thick rachis and pinnule shape, and since there are no other ferns known from this TC.

Among the five sterile species of *Cladophlebis* and the four additional sterile genera of fern fronds at the type locality (Umk 111), there are no obvious affiliations with *A. killickii*.
Holotype PRE/F/400a
Holotype PRE/F/400b
PRE/F/18820
PRE/F/18820
PRE/F/8374
PRE/F/6373
PRE/F/6374
PRE/F/18820

Umkomaas Valley (Umk 111 Dic 2sp)

MARATTIALES

Asterotheca killickii
**Osmundopsis** Harris 1931

**Type species**

*Osmundopsis sturi* (Raciborski 1890–1891) Harris 1931. Grojec, near Cracow, Poland; Jurassic.

**Generic concept**

An osmundaceous fern with cladophleboid sterile pinnules and fertile pinnules comprising much reduced or absent laminae bearing adjacent clusters of sporangia.

**Generic characters**

*Fertile foliage*: frond bipinnate; pinnules with much reduced or absent lamina; sporangia in irregular clusters, closely placed on either side of the midvein, apical region with thickened cell walls (annulus), dehiscing by a longitudinal slit.

*Sterile foliage*: frond bipinnate; pinnules with cladophleboid venation, lateral veins well-spaced and once-forked.

**Plant**: medium-sized fern with fronds radiating from a rhizomatous base.

**Etymology**

*Osmundopsis*—a fossil genus close to the extant genus *Osmunda*.

**Global range**: Numerous species, Pangaea, P.–J. Gondwana Triassic occurrence

**Frequency** (*F*): 5 degree squares (of the 84 across Gondwana).

**Ubiquity** (*U*): 3 continents (of 5 comprising Gondwana).

**Diversity** (*D*): 4 species.

**Abundance** (*A*): <1% (the norm in Molteno TCs).

**Longevity** (*L*): 7 myrs (lower Anisian–mid-Carnian).

**Colonisation success**: FUDAL rating 5/3/4/-/7 = 19.

**Endemism**: fairly widespread in Eastern Gondwana.

**Molteno occurrence**

**Frequency** (*F*): 6 TCs (of the 100 sampled in the Molteno).

**Diversity** (*D*): 4 species.

**Abundance** (*A*): 18 indivs total, very rare to extremely rare.

**Habit**: based on Antarctic (Phipps et al. 1998) and Australian (Holmes 2001) fossils, possibly similar to extant *Osmunda*, i.e. rhizomatous with numerous fronds.

**Preferred habitat**: no preference indicated as each record occurs in a distinct Molteno habitat.

**Affiliation (fertile & sterile fronds)**

Phipps et al. (1998) described some beautifully preserved *Osmunda clavatontites* specimens from the Triassic of the Allan Hills, Antarctica. These show fertile and sterile pinnules attached to the same frond.

Holmes (2001) has some excellent affiliated material for *Osmundopsis scalaris*. This consists of the holotype (AMF 113468) with some seven fronds (two partially fertile) that radiate from a common base to show the form of growth. Another specimen (AMF 113447) shows fronds attached to a rhizome.

In the Molteno, *Osmundopsis* affiliations are possible at the following 3 TCs:

- **Umk 111**: *O. petiolaris* and *Cladophlebis moltenensis*—Grade 3 (Mut. occ.) (another possibility could be *Stormbergia*);

- **Kon 211**: *O. sp. cf. O. scalaris* may be affiliated with *C. barbara*, as the most common sterile foliage (of *Cladophlebis* morphology) is already affiliated with *Rootiodites pulchra*. (However, the latter sterile foliage is very similar to the sterile fronds described as *O. scalaris* from Nymboida, Australia). The other sterile fronds at this TC, *Parsorophyllum africana* and *Sphenopteris annakatiae*, are unlikely to be affiliated with *Osmundopsis*.

- **Pen 311**: *O. botryoides* and *C. rosemariae* are the only fertile and sterile ferns respectively found and may thus be affiliated, but *C. rosemariae* also occurs at another 14 TCs that have not as yet yielded fertile *Osmundopsis*.

- **Aas 411**: where 10 specimens of *O. racemosus* occur; there are no *Cladophlebis*-type sterile ferns and only two other sterile ferns (Tab. 6) that are not yet affiliated with fertile fronds.
Classification & comparison

Suprageneric classification (Osmundaceae/Osmundales)

The presence of a group of thickened cells forming an annulus on the sporangium places *Osmundopsis* in the order Osmundales and the family Osmundaceae.

Intergeneric comparison

Harris (1931) created the genus *Osmundopsis* for fossil ferns that were similar to the extant genus *Osmunda* but lacked certain preservational details of the sporangia. (Note that the genus *Osmundites* is used for fossil fern stems.) Later, Harris (1961) stated ‘it is possible that the differences (i.e. from *Osmunda*) are insufficient to differentiate a valid genus’. Phipps et al. (1998) used the extant genus *Osmunda* in describing well-preserved Antarctica Triassic fossils (with sporangia) and stated that ‘*Osmundopsis* is intermediate in form between *Todites* and *Osmunda*’. Until more details of the sporangia are available, we prefer to use the genus *Osmundopsis sensu Harris* (1931) for our Molteno material. For the Gondwana ‘geostrat’ distribution, we have included the Antarctica material, *Osmunda claytoniana*, under *Osmundopsis*.

Interspecific comparison

*Osmunda claytoniana* (Phipps et al. 1998), from the Triassic of Antarctica is close to the extant *O. claytoniana* and also to *Osmundopsis scalaris* Holmes (2001) from Australia. Both fossil species are well known from fertile and sterile material occurring on the same frond.

The four Molteno species included here are highly varied in regard to the arrangement, size and morphology of the sporangia or synangia—to the extent that they might each be included in different genera. Whilst *O. petiolaris* and *O. racemosus* could end up being placed in two widely distinct genera of fern-like gymnosperms, *O. botryoides* and *O. sp. cf. scalaris* show similarities to the sporangia of *Birtodites*.

Comparisons beyond Gondwana Triassic

Fossil ferns (see above)

Van Konijnenburg-van Cittert (2000) reviewed the occurrence of osmundaceous spores through time and also described two *Osmundopsis* species (Van Konijnenburg-van Cittert 1996) from the Yorkshire Jurassic.

Extant ferns

The genus *Osmunda* has fertile and sterile fronds closely similar to those of the fossil material.

Rarity & quality of the Molteno fertile material (Tab. 14)

Of the four *Osmundopsis* species, three are known only from the RP. Very dubious, poorly preserved individuals of the fourth species, *O. petiolaris*, occur from two further localities. Each of the four species is effectively represented by only a single variously convincing fertile specimen: the material is very rare to extremely rare (Tab. 9).

O. *botryoides* (Pen 311, pls 113–115): though just one small fragment is known, it is beautifully preserved and clearly shows the arrangement and morphological details of the sporangia.

O. *sp. cf. scalaris* (Kon 211): whilst the single available individual of this species is less fragmentary than that for *O. botryoides*, it is very much less adequately preserved—the arrangement and morphology of the sporangia are just discernable in some pinnules (pls 111(3, 4), 112 (2, 3).

O. *petiolaris* (Umk 111, pl. 116): only the holotype is convincing; the additional two individuals are poorly preserved fragments and are included in this species very uncertainly. The two individuals and the single individual from the two sister palaeodemes, Cyp 111 and Kon 222 respectively, are likewise poorly preserved fragments and are included here with obvious reservation.

O. *racemosus* (Aas 411, pls 117, 118): though all 10 individuals comprising the RP are listed here (see also Tab. 9) as fertile, only the holotype (pl. 118) shows structures interpreted as sporangia.
**Osmundopsis botryoides** H.M. And. & J.M. And., sp. nov

**Holotype**
Specimen: PRE/F/16892a,b; pls 113–115.
Assemblage: Pen 311 Hei elo, Peninsula (Campsite Quarry).
Preservation: a partial pinnate frond, with counterpart; impression in thinly laminated buff shale.

**Reference palaeodeme**
Assemblage (TC): as for holotype.
Specimens: 1 indiv. (1 partial), pls 113–115.

**Sister palaeodemes**—nil.

**Specific diagnosis**
An *Osmundopsis* species with at least 11 pairs of pinnules bearing 1–4 sporangial clusters in a compact head on strongly reduced lamina.

**Specific characters**
Fertile foliage: frond unknown; pinnae length unknown; pinnules with strongly reduced lamina, bearing 1–4 sporangial clusters, each consisting of 3–5 sporangia; sporangia large (0.5 mm diam.), annulus distal, rays gracile and forking, dehiscence rib linear and distinct.

Sterile foliage: unknown.

**Etymology**
botrys—(Gr.) cluster, with reference to the sporangial clusters.

**Comment & comparison**
This species, represented by a single beautifully preserved individual, is distinguished from the other Molteno *Osmundopsis* species by having not more than 4 sporangial clusters per pinnule. The thickened cells of the sporangia are clearly preserved and spores are visible in distinct masses alongside the sporangia, pl. 115(1, 2). The individual sporangia are, in their ornamentation, very like those of *Birtodites*, and it could be argued that this species is more closely allied to that genus than to *Osmundopsis*. However, as *Osmundopsis* has a very reduced lamina it is retained here.
**Osmundopsis sp. cf. O. scalaris** Holmes 2001

**Holotype**

*Specimen*: AMF 113468, Australian Museum, Sydney.

*Assemblage*: Coal Mine Quarry, Nymboida, Basin Creek Fm., Nymboida C.M., NSW, Australia; Ladinian, M. Triassic.

*Preservation*: an almost complete frond that radiates with six others from a common base, no cuticle preserved, fine siltstone poorly bedded.

**Reference palaeodeme (RP)**

*Assemblage (TC)*: as for holotype.

*Specimens*: 17 indiv mentioned (mostly intact with some fronds attached to a rhizome), Holmes 2001, figs 19–21.

**Molteno reference specimen**

*Specimen*: PRE/F/14477a,b; pls 111, 112.

*Assemblage*: Kon 211 Ast 2 spp, Konings Kroon.

*Preservation*: a partial intact fertile frond, with counterpart; impression in massive light grey shale with poor cleavage.

**Sister palaeodemes (Molteno)—nil.**

**Specific concept**

An *Osmundopsis* species bearing pinnae with at least 12 pairs of pinnules bearing 8–10 sporangial clusters on strongly reduced lamina.

**Specific characters** (based on Nymboida RP, except for sporangia)

*Fertile foliage*: frond bipinnate, ca 500 mm long, with fertile pinnae in middle portion; pinnae with pinnules in 12 or more pairs, pinnules with nearly completely reduced lamina, bearing at least 8–10 sporangial clusters; sporangia (based on Kon 211) relatively large, 0.5 mm diam., in clusters of 4 or 5; annulus distal, rays gracile; dehiscence rib linear distinct.

*Sterile foliage*: see Holmes (2001); unknown from the Molteno.

**Etymology**

*scalaris*—(Lat.) ladder-like, referring to the appearance of the fertile pinnae.

**Comment & comparison**

The single individual from the Molteno, although attractive photographically, has poorly preserved sporangia. It is preserved with manganese dioxide dendrites that look at first glance confusingly like sporangia extruding into the matrix from the actual sporangia, pls 111, 112.

*Osmundopsis sp. cf. O. scalaris* is the only Molteno species with a thick rachis and attached pinnae. In this aspect it is similar to *Osmunda claytoniites* from Antarctica (Phipps et al. 1998) that has a frond preserved with both fertile and sterile pinnae attached to a thick rachis. However, *Osmunda claytoniites* differs from *Osmundopsis scalaris* by the fertile pinnules being irregular, more compact and less in number. The fertile pinnules of the Molteno specimen are closely similar to *O. scalaris* but to date the sterile pinnules are unknown. Though we have included our single fertile frond fragment from the Molteno in the same species as the far more complete material from Nymboida, Australia, this is done with uncertainty. The Molteno specimen differs in a few respects: the primary axis is a little over twice the diameter and the pinnule pairs appears to be far fewer. The other Molteno species are known only from smaller pieces and differ by having less than 8 sporangial clusters or, in the case of *O. petiolaris*, having a distinct petiole to the pinnule.
Osmundopsis petiolaris H.M. And. & J.M. And., sp. nov.

**Holotype**

*Specimen:* PRE/F/405a,b; pl. 116.

*Assemblage:* Umk 111 Dic 2 spp., Umkomas Valley.

*Preservation:* a partial bipinnate frond, with counterpart; compression in thinly laminated, carbonaceous (cuticle), medium dark grey shale with good cleavage.

**Reference palaeodeme**

*Assemblage* (TC): as for holotype.

*Specimens:* 3 indivs (1 partial, 2 frags), pl. 116.

**Sister palaeodemes—2**

Cyp 111 Dic cra: 2 indivs (2 frags).

Kon 222 Dic odo: 1 indiv. (1 partial).

**Specific diagnosis**

A putative *Osmundopsis* species with petiolate pinnules bearing 8–10 sporangial clusters on partially reduced lamina with strong midrib but no lateral veins.

**Specific characters**

Fertile foliage: *frond* bipinnate, incompletely known; *pinnules* petiolate, lamina partially reduced with strong midrib but no clear lateral veins, bearing 8–10 sporangial clusters (?synangia); ?synangia ca 10 mm in diam., each consisting of 3 or 4 ?sporangia; ?sporangia medium, 0.3–0.5 mm diam., details unknown.

Sterile foliage: unknown, but see note below.

**Etymology**

*petiolaris*—referring to the petiolate pinnules.

**Comment & comparison**

This species is distinguished from *Osmundopsis racemosus* and *O. botryoides* in having 8–10 sporangial clusters and from *O. sp. cf. O. scalaris* by its petiolate form.

The type specimen clearly shows an apparent petiole to the pinnules. This is interpreted as the basal portion of the midvein that does not bear sporangial clusters. Two additional specimens from Umk 111 are placed in this species but due to their incompleteness do not show the apparent petiole. The specimen from Kon 222 (BP/2/3956) is not very clear but shows an apparent constriction at base.

With the sporangial details of this species quite uncertain, the relationships of *O. petiolaris* remain enigmatic. It may even be that we are dealing with another of the great diversity of Molteno gymnosperms rather than with a fern.

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**Osmundopsis petiolaris**

Holotype

*Specimen:* PRE/F/405a,b; pl. 116.

*Assemblage:* Umk 111 Dic 2 spp., Umkomas Valley.

*Preservation:* a partial bipinnate frond, with counterpart; compression in thinly laminated, carbonaceous (cuticle), medium dark grey shale with good cleavage.

**Reference palaeodeme**

*Assemblage* (TC): as for holotype.

*Specimens:* 3 indivs (1 partial, 2 frags), pl. 116.

**Sister palaeodemes—2**

Cyp 111 Dic cra: 2 indivs (2 frags).

Kon 222 Dic odo: 1 indiv. (1 partial).

**Specific diagnosis**

A putative *Osmundopsis* species with petiolate pinnules bearing 8–10 sporangial clusters on partially reduced lamina with strong midrib but no lateral veins.

**Specific characters**

Fertile foliage: *frond* bipinnate, incompletely known; *pinnules* petiolate, lamina partially reduced with strong midrib but no clear lateral veins, bearing 8–10 sporangial clusters (?synangia); ?synangia ca 10 mm in diam., each consisting of 3 or 4 ?sporangia; ?sporangia medium, 0.3–0.5 mm diam., details unknown.

Sterile foliage: unknown, but see note below.

**Etymology**

*petiolaris*—referring to the petiolate pinnules.

**Comment & comparison**

This species is distinguished from *Osmundopsis racemosus* and *O. botryoides* in having 8–10 sporangial clusters and from *O. sp. cf. O. scalaris* by its petiolate form.

The type specimen clearly shows an apparent petiole to the pinnules. This is interpreted as the basal portion of the midvein that does not bear sporangial clusters. Two additional specimens from Umk 111 are placed in this species but due to their incompleteness do not show the apparent petiole. The specimen from Kon 222 (BP/2/3956) is not very clear but shows an apparent constriction at base.

With the sporangial details of this species quite uncertain, the relationships of *O. petiolaris* remain enigmatic. It may even be that we are dealing with another of the great diversity of Molteno gymnosperms rather than with a fern.
**Osmundopsis racemosus** H.M.And. & J.M.And., sp. nov.

**Holotype**

*Specimen*: PRE/F/21642a,b; pl. 118.

*Assemblage*: Aas 411 Dec SpH: Aasvoëlberg.

*Preservation*: a partial pinnate frond, with counterpart; impression in thinly laminated, strongly baked yellowish grey shale with very good cleavage.

**Reference palaeodeme**

*Assemblage* (TC): as for holotype.

*Specimens*: 10 indivs (10 partial), pls 117, 118.

**Sister palaeodemes**—nil.

**Specific diagnosis**

A putative *Osmundopsis* species with sessile pinnules bearing ca 6 sporangial clusters on partially reduced lamina still showing venation.

**Specific characters**

*Fertile foliage*: frond bipinnate, incompletely known; pinnules constricted at base, lamina partially reduced, showing midrib and forking lateral veins, bearing ca 6 sporangial clusters (?synangia); ?synangia ca 2 mm diam., fan-shaped with ca 6 lobes; ?sporangia ca 1 mm long by 0.1 mm diam., narrowly wedge-shaped, details unknown.

*Sterile foliage*: unknown.

**Etymology**

*racemosus*—(Lat.) full of clusters, with reference to the sporangial clusters.

**Comment & comparison**

This species is distinguished from *Osmundopsis petiolaris* and *O. botryoides* in having 6–8 sporangial clusters and from *O. scalaris* in its partially modified pinnule laminae.

The part and counterpart of various specimens within the palaeodeme show either the venation or the clusters of sporangia better displayed. The individuals PRE/F/21654b’x’, c’y’, pl. 117(2, 3), show the dorsal view of the pinnule laminae and it is the bulging nature of these laminae that suggests their being fertile. It is also possible that a degree of galling may be involved.

As this is the only fertile Molteno *Osmundopsis* species that shows the venation of the pinnules, there may be doubts as to whether it is correctly placed in that genus. As for *O. petiolaris*, it is quite possible that this species is gymnospermous rather than fern—with the wedge-shaped putative sporangia proving to be seeds.
Rootiodites H.M. And. & J.M. And., gen. nov.

Type species
Rootiodites pulchra H.M. And. & J.M. And., sp. nov.

Generic diagnosis
An osmundaceous fern with cladophleboid pinnules bearing groups of closely adjacent sporangia along the lateral veins and covering about half the lamina surface.

Generic characters
Fertile foliage: frond bipinnate; pinnules entire to lobed; sporangia closely adjacent, in groups along the lateral veins and covering about half the lamina surface.

Sterile foliage: frond bipinnate; pinnules with cladophleboid venation; lateral veins mainly once forking, occasionally twice.

Eymology
Rootiodites—contrived in part after the farm Rooipoort on which the fossils were found, and Todites the fossil genus similar to the extant genus Todea.

Global range: 2 spp, Gondwana, Tr. (CRN).

First & last: the Molteno species described here.

Gondwana Triassic occurrence
Frequency (F): 5 degree squares (of the 84 across Gondwana).
Ubiquity (U): 2 continents (of 5 comprising Gondwana).
Diversity (D): 4 species.
Abundance (A): 18% (the norm in Molteno TCs).
Longevity (L): 3 myrs (lower–mid-Carnian).

Colisation success: FDAL rating 5/2/4/18%/3 = 32.
Endemism: W. Gondwana endemic.

Molteno occurrence
Frequency (F): 6 TCs (of the 100 sampled in the Molteno).
Diversity (D): 2 species.
Abundance (A): 63% to 1 indiv., co-dominant to very rare.

Habit: rhizomatous with fronds up to 1 m long; based on the reconstruction of the whole-plant of R. integra fossils from Kan 111.

Preferred habitat: Fern/Kannaskoppia meadow (Molteno habitat 7), based on R. integra occurring at Kan 111; however, Rootiodites has also been collected from four other habitats.

Affiliation (fertile & sterile fronds)
Sterile and fertile pinnules occur on the same frond in the type specimen of Rootiodites pulchra. For R. integra, fertile and sterile fronds are closely associated with in situ rhizomes at Kan 111 and the affiliation is rated grade 4.

Classification & comparison
Suprageneric classification (Osmundaceae/Osmundales)
Rootiodites is placed in the order Osmundales and family Osmundaceae based on the relatively small sporangia not forming distinct synangia or sori.

Intergeneric comparison
None of the following four genera have sporangia in distinct small groups between the midvein and margin as occurs in Rootiodites:

Todites and Elantodites (this volume) have sporangia covering the entire pinnule;

Nymbofelicia Holmes (2001) has sporangia in loose aggregates of 10–15 forming sori centred below the fork of each lateral vein;

Birtodites (this volume) has larger sporangia and in regular groups covering the entire pinnule.

The genus Chansitheca (Andrews et al. 1970, p. 297) has 4–6 oval sori composed of 8–12 sporangia on each side of the midvein of the pinnule. The sporangia are ca 0.2 mm in diameter with a distinct equatorial annulus as in Gleichenia. Chansitheca, a genus based on Late Carboniferous material from China, was used by Herbst (1963) for Triassic fern material from Argentina that he named C. argentina. As no sporangial structure is preserved, Herbst’s material does not fit the generic diagnosis of Chansitheca. This Argentinean material may be better placed in the new Molteno genus Rootiodites.

The genus Coniopteris (Harris 1961; Andrews et al. 1970) has pinnules with a reduced lamina, a distinct indusium and sporangia with a well-developed annulus. None of these characters are evident in the fern Coniopteris harringtoni (Morel et al. 1992) that we identify as Rootiodites sp.

Interspecific comparison
Chansitheca argentina (Herbst 1963) is here reclassified as Rootiodites argentina (Herbst) comb. nov. and differs from the Molteno species by the longer pinnules and more groups of sporangia. Coniopteris harringtoni (Morel et al. 1992, pl. 1, fig. b) is here placed in Rootiodites sp., but the illustration is insufficient to make a specific comparison (Tab. 4).

In neither of the two described Molteno species are the sporangia sufficiently clearly preserved at high magnification to enable good close-up photography, or particularly sound interpretation of the morphology. Whilst R. pulchra and R. integra are readily placed within the same genus on the basis of pinna shape and sporangial arrangement, the individual sporangia are possibly quite different.
Though a fair number of *Rooitodites* specimens are fertile (7 indivs from 4 TCs for *R. pulchra* and 18 indivs from 2 TCs in *R. integra*), no single specimen shows the individual sporangia clearly preserved. We have not succeeded in taking higher magnification photos of these sporangia and do not draw their close-up morphology in pen sketches. It is uncertain whether *R. pulchra* sporangia are more like those in *R. integra* or possibly those in *Birtodites*.

*R. pulchra* (Kon 211/221): in the four fertile individuals from this TC the arrangement of the sporangia shows up well, and on one of these (BP/2/4211b, pls 119, 120) the dehiscence lines show up reasonably well, but the ?annulus is just faintly visible on a few sporangia as shown [circled on pl. 120(2)]. The single fertile specimen from each of the 3 SPs (Kon 222, Mat 111 and Aas 111) shows no sporangial details.

*R. integra* (Kan 111): the two smallish fragments illustrated (pls 121, 122) show well the distribution of the sporangia on the pinnae, but only on a few sporangia on a single pinna (PRE/F/13345a, b pls 16(1), 17(1)) and see p. 57. The single fertile specimen from each of the 3 SPs (Kan 111 and Aas 111) shows no sporangial details.

### Rarity & quality of fertile Molteno material (Tab.15)

<table>
<thead>
<tr>
<th>assemblages (taphocoenoses)</th>
<th><em>R. pulchra</em> (Kon 211/221)</th>
<th><em>R. integra</em> (Kan 111)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Kan 111 Ast spA</td>
<td>-</td>
<td>17 63</td>
</tr>
<tr>
<td>Tel 111 Hei elo</td>
<td>-</td>
<td>1</td>
</tr>
<tr>
<td>Kon 222 dic odo</td>
<td>1 1</td>
<td>-</td>
</tr>
<tr>
<td>Kon 211/222 Ast 2sp</td>
<td>4 25</td>
<td>-</td>
</tr>
<tr>
<td>Mat 111 Dic dub</td>
<td>1 3</td>
<td>-</td>
</tr>
<tr>
<td>Aas 111 Hei elo</td>
<td>1 1</td>
<td>-</td>
</tr>
<tr>
<td>Total TCS</td>
<td>4 3</td>
<td>2 1</td>
</tr>
<tr>
<td>Total indivs</td>
<td>7 25</td>
<td>18 63</td>
</tr>
</tbody>
</table>

R. *pulchra* (Kon 211/221): in the four fertile individuals from this TC the arrangement of the sporangia shows up well, and on one of these (BP/2/4211b, pls 119, 120) the dehiscence lines show up reasonably well, but the ?annulus is just faintly visible on a few sporangia as shown [circled on pl. 120(2)]. The single fertile specimen from each of the 3 SPs (Kon 222, Mat 111 and Aas 111) shows no sporangial details.

*R. integra* (Kan 111): the two smallish fragments illustrated (pls 121, 122) show well the distribution of the sporangia on the pinnae, but only on a few sporangia on a single pinna [PRE/F/13355a, pl. 122(1–5)] on the one specimen, is the morphology of the annulus imperfectly discernable. Whilst two or three of the remaining 15 fertile specimens in the Kan 111 RP show some faint sporangial details, they add nothing to the material illustrated. The single fertile fragment from the Tel 111 SP shows no sporangial details.
**Rooitodites pulchra** H.M. And. & J.M. And., sp. nov.

**Holotype**

*Specimen:* BP/2/4211 ‘z’, a; pls 119, 120.

*Assemblage:* Kon 211/221 Ast 2 spp, Konings Kroon.

*Preservation:* partial fertile frond, labelled ‘z’, with counterpart; closely associated with another two fronds in the same block, pl. 8(3). The frond above ‘z’ is labelled ‘y’ and is also fertile, pls 6, 7, while ‘x’ lying above the type ‘z’ is a sterile frond, pl. 8(1, 2). The same orientation and close proximity of the fronds indicates they may be parts of a single plant; impression in massive light grey shale with poor cleavage.

**Reference palaeodeme**

*Assemblage* (TC): as for holotype.

*Specimens:* 4 indiv. fertile (2 intact, 2 partial), 25% of TC sterile fronds (almost complete to partial), pls 6–11, 119, 120.

**Sister palaeodemes—3**

Mat 111 Dic dub: 1 indiv. fertile (partial); 3 indivs sterile (2 intact, 1 partial).

Kon 222 Dic odo: 1 indiv. fertile (frag.); 1 indiv. sterile (partial).

Aas 111 Hei elo: 1 indiv. fertile (intact).

**Specific diagnosis**

A *Rooitodites* species bearing distinct groups of sporangia which commence from base of proximal pinnules and spread apically and distally.

**Specific characters**

Fertile foliage: *frond* bipinnate, estimated length 200 mm; *fertile pinnules* occurring in basal portion of frond; *fertile pinnules* bearing sporangia centred about the mostly once-forked lateral veins (on the fertile pinnules the veins are not clearly preserved), distal fertile pinnules with proximal sporangia only; *sporangia* small, 0.3 mm diam., closely adjacent in groups of 4–12; *annulus* distal, morphology uncertain; *dehiscence* line clear, linear to imperfectly y-shaped.

Sterile foliage: *frond* bipinnate, length ca 300 mm or more; *pinnules* entire to lobed, *L:W* ratio 2–3:1; *venation* showing a clear midrib, lateral veins usually once-forking sometimes twice.

**Etymology**

*pulchra* (Lat.)—beautiful, referring to the beautifully preserved fertile frond of the type specimen.

**Comment & comparison**

The type specimen of *Rooitodites pulchra* occurs in a block, tf. 3 on p. 55, pl. 8(3), closely associated with two further fronds, one fertile the other sterile. Both fertile fronds show the fertile pinnules on the basal portion of the frond, with the fertile pinnules occurring proximally on the pinnules (distally the sporangia occur only on the basal portion of the pinnules).

*R. pulchra* is distinguished from the fertile fronds of *R. integra* by the lower *L:W* ratio of the pinnules and by the groups of sporangia that commence from the base of the proximal pinnules and spread apically and distally—whereas in *R. integra* the sporangia appear to commence from the apical area of the pinnule and spread proximally. As all the better-preserved fertile pinnae of *R. integra* are detached, their position on the frond is unknown.

The single specimen from Aas 111, Hei elo (BP/2/4281), has poorly preserved sporangia and its identity is uncertain. Possibly affiliated sterile fronds from the same TC have been placed in *Cladophlebis janetae*.
Rooitodites pulchra

Showing position of fronds ‘x’, ‘y’ and ‘z’ (the holotype), occurring at different levels in the same block.
**Rooitodites integra** H.M.And. & J.M.And., sp. nov.

**Holotype**
Specimen: PR/F/13355a,b; pl. 122.
Assemblage: Kan 111 Ast spA, Kannaskop.
Preservation: partial fertile frond with counterpart; impression in thick-bedded, moderately baked, greenish grey, silty mudstone with very poor cleavage.

**Reference palaeodeme**
Assemblage (TC): as for holotype.
Specimens: 17 indivs fertile (2 intact, 12 partial, 3 frags), 63% of TC sterile fronds (intact to partial), pls 12–18, 121, 122.

**Sister palaeodemes—1**
Tel 111 Hei elo: 1 indiv. fertile (partial), pl. 19.

**Specific diagnosis**
A *Rooitodites* species bearing distinct groups of sporangia, which commence from apical area of pinnule and spread proximally.

**Specific characters**
*Fertile foliage:* frond bipinnate, length probably similar to sterile foliage; fertile *pinnae* in unknown position along rachis; *pinnules* bearing sporangia centred about the mostly unforked lateral veins and which commence from apical area of pinnule and spread proximally; sporangia small, 0.2–0.25 mm diam., closely adjacent in distinct groups of 6–12; *annulus* distal, morphology uncertain; dehiscence not evident.

*Sterile foliage:* frond bipinnate, length ca 1.5 m; *pinnules* entire to lobed, L: W ratio 3.5–4:1; venation showing clear midrib, lateral veins usually once-forking and rarely twice.

**Etymology**
*integra* (Lat.)—whole or complete, referring to specimens from the type locality which include portions of a complete plant.

**Comment & comparison**
For comparison with *Rooitodites pulchra* see text for that species.

A single fertile frond from Tel 111 that is identified as *R. integra* has ca 7 distinct groups of only 4–6 adjacent sporangia and also shows some cell structure (pl. 19). From the same TC are two sterile leaves that are identified as *Cladophlebis rosemariae*. They show similar cell structure and are thus possibly affiliated with the fertile frond.

As the better fertile pinnae of *R. integra*, are detached specimens, their form of attachment to the rachis is not known. One specimen, showing the lower portions of three radiating rachises, has a well-preserved fertile pinna in correct alignment to one rachis but with the point of attachment missing. Other pinnae on this rachis appear to be fertile and attached but are not well preserved.

The total length of the fronds is estimated at ca 1.5 m based on specimens figured on pls 17(1), 18 and others. These fronds have no pinnae attached on the basal 1/3 to 1/5 of their length. The lower pinnae are short (ca 60 mm) then increase in length to mid-frond (ca 120 mm) where they are attached at a high angle. Apically the pinnae decrease in length and become more acutely attached (PRE/F/13327b).

Together with the portions of fertile and sterile fronds were numerous rachis bases attached to in situ rhizomes in a fossil soil horizon (pl. 18[2]). The reconstruction of the complete fern is based on the associated presence of all these specimens. The uniquely attached ovulate organs, foliage and stems of the gymnospermous plant *Kannaskoppia* (And. & And. 2003; pp 286–313) occurs in this same assemblage.

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Habit sketch based on the fossil fronds and rhizomes from Kan 111 and the extant *odea barbara*. 

**Rooitodites integra**

PRE/F/13345a,b
pl. 16(1), 17(1)
Holotype
Rooitodites pulchra

pl. 6

Konings Kroon
(Kan 211/221 Ast 3app)

all BP/2/4211'y/a

OSMUNDALES
Konings Kroon
(Kon 211/221 Ast 2spp)

Rooitodites pulchra
Konings Kroon
(Kon 211/221 Ast 2spp)

Rooitodites pulchra

BP/2/4192

PRE/F/10272
(figs 2, 3)

PRE/F/10269b
Konings Kroon
(Kon 211/221 Ast 2spp)
Konings Kroon
(Kon 211/221 Ast 2 spp)
Rooitodites integra

Kannaskop
(Kan 111 Ast spA)

PRE/F/13371 (figs 1, 2)

PRE/F/13365 (figs 3, 4)

PRE/F/13362a (figs 5, 6)
Kannaskop (Kan 111 Ast spA)
Rooitodites integra

pl. 14

OSMUNDALES

Kannaskop
(Kan 111 Ast spA)
Kannaskop
(Kan 111 Ast spÃ­)

all PRE/F/13346b
Kannaskop
(Kan 111 Ast spA)
**OSMUNDALES** Bromhead 1838

**OSMUNDACEAE** Brecht. & J. Presl 1820

**Birtodites** H.M. And. & J.M. And., gen. nov.

**Type species**

*Birtodites holmesii* H.M. And. & J.M. And. sp. nov., Bir 111 Sph 2 spp, Birds River, Karoo Basin, S. Africa; Carnian, Triassic.

**Generic diagnosis**

An osmundaceous fern with fertile pinnules bearing a row of closely spaced sporangia aligned on either side of the lateral veins and covering nearly the entire lamina.

**Generic characters**

*Fertile foliage:* frond bipinnate, length unknown; pinnules oblong, L:W ratio 2–3:1, bearing a row of 2–4 closely-spaced sporangia aligned on either side of each lateral vein and covering nearly the entire lamina; sporangia large, 0.5 mm diam., attachment sessile, circular to broadly oval; annulus distal and strongly developed (arcuate) with rays of thickened cells irregularly bean-shaped; dehiscence area prominent with very distinctive ribbed band of linear thickened cells running its full length.

*Sterile foliage:* unknown.

**Etymology**

*Birtodites*—contrived from the type locality, Birds River and Todites, a fossil fern similar to the extant genus *Todea*.

**Global range:** 1 sp., Gondwana, Tr. (CRN).

**First & last:** the single Molteno species described here.

**Gondwana Triassic occurrence**

*Frequency (F):* 2 degree squares (of the 84 across Gondwana).

*Ubiquity (U):* 1 continent (of 5 comprising Gondwana).

*Diversity (D):* 1 species.

*Abundance (A):* <1% (the norm in Molteno TCs).

*Longevity (L):* 2 myrs (lower Carnian).

*Colonisation success:* FUDAL rating 2/1/1/-/2 = 6.

*Endemism:* Molteno Fm. endemic.

**Molteno occurrence**

*Frequency (F):* 3 TCs (of the 100 sampled in the Molteno).

*Diversity (D):* 1 species.

*Abundance (A):* 23 indivs, extremely rare.

*Habit:* none suggested as sterile fronds are unknown.

*Preferred habitat:* Sphenobaiera woodland.

**Affiliation**

(fertile & sterile fronds)

The affiliation of *Birtodites* with *Birmoltia* (grade 2) is problematic and further evidence is required. The Bir 111 and Aas 411 TCs (both lake deposits) are unusual in yielding a relatively large number of fertile fern fronds and fewer sterile ones. At Bir 111, some 50 sterile fronds are clearly affiliated with *Elantodites stuartii*, while *Birmoltia intervenatus* (11 indivs), *Cladophlebis paucinerva* (2 indivs) and *C. janetae* (2 indivs) are all possible affiliates. At Aas 411 one sterile specimen is affiliated with *Elantodites stuartii*, and the remaining two specimens belong to *Nymboidiumtum schwyzeri* and *Molteniella terblanchiorum*. At Lit 111, the sterile ferns are *C. evelynae* (1 indiv.) and *N. schwyzeri* (9 indivs). At Bir 111, the most likely affiliate is *Birmoltia intervenatus*, while for Aas 411 and Lit 111, *N. schwyzeri* is suggested.

**Classification & comparison**

**Suprageneric classification** (Osmundaceae/Osmundales)

The thickened apical cell walls of the sporangia and dehiscence by a longitudinal slit are the defining characters for placing *Birtodites* in the order Osmundales and family Osmundaceae. For comparison see the SEM photo of extant *Osmunda* sporangia showing the open longitudinal line of dehiscence in Foster & Gifford (1974, p. 341).

**Intergeneric comparison**

*Birtodites* differs from *Rootodites* and *Elantodites* by the alignment of the sporangia around the lateral veins and by the larger sporangia with a distinct longitudinal slit.
Rarity & quality of fertile Molteno material (Tab. 16)

*Birtodites* is relatively well represented by fertile material (23 indivs from 3 TCs). Even so, the number of individuals showing sporangia with clearly preserved morphology is remarkably few.

*Bir 111* (with 8 fertile indivs): of the 8 fertile frond fragments, mostly generally clearly preserved, just the one (pls 123–125) shows the finely preserved sporangial morphology.

*Lit 111* (with 2 fertile indivs): specimen BP/2/1712, pl. 25(7), shows some sporangial morphology. This material is carbonaceous and may yield spores on maceration.

*Aas 411* (with 13 fertile indivs): whilst three particular specimens (pls 127, 128) show the sporangia in sharply defined outline with well-pronounced dehiscence lines, only one of these includes a very limited number of individual sporangia with reasonably clearly developed distal rays of thickened cells.

### Tab. 16. *Birtodites*, Molteno occurrence

<table>
<thead>
<tr>
<th>assemblages (taphocoenoses)</th>
<th><em>B. holnessae</em> (Bir 111)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>*</td>
</tr>
<tr>
<td>Bir 111 Sph 2spp</td>
<td>0</td>
</tr>
<tr>
<td>Lit 111 Dic/Hei</td>
<td>2</td>
</tr>
<tr>
<td>Aas 411 Dic/Sph</td>
<td>13</td>
</tr>
<tr>
<td>Total TCs</td>
<td>3</td>
</tr>
<tr>
<td>Total indivs</td>
<td>23</td>
</tr>
</tbody>
</table>

The Molteno floodplain biome showing the position of the *Birtodites* habitats

References:
Cairncross et al. 1995
And. & And. 2003. (p. 39)
**Birtodites holmesii** H.M. And. & J.M. And., sp. nov.

**Holotype**

*Specimen*: PRE/F10709a, b; pls 20, 22, 23, 123–125.

*Assemblage*: Bir 111 Sph 2 spp., Birds River.

*Preservation*: virtually complete pinna and portion of a second pinna, with counterpart; impression in thinly laminated, yellowish grey shale with very good cleavage.

**Reference palaeodeme**

*Assemblage* (TC): as for holotype.

*Specimens*: 8 indivs (1 intact, 3 partial, 4 frags), pls 20–23, 123–126.

**Sister palaeodemes**—2

Aas 411 Dic/Sph.: 13 indivs fertile (10 partial, 3 frags), pls 24, 25(1, 2), 127, 128.

Lit 111 Dic/Hei: 2 indivs fertile (2 frags), pl. 25(3–7).

**Specific diagnosis**

As for genus.

**Specific characters**

As for genus.

**Eponym**

*holmesii*—for Keith Holmes, Australian palaeobotanist, in warm appreciation for his manifold assistance in the preparation of this volume.

**Comment & comparison**

At Bir 111, the type locality, the sporangia are well preserved and show clearly the longitudinal line of dehiscence (pls 20–23, 123–125) though most are still intact and had not released their spores prior to fossilisation.

At Aas 411 (SP), with 13 fertile individuals, the sporangia do not generally cover the pinnule surface as fully as in the Bir 111 RP. In consequence, the arrangement of the sporangia is somewhat more evident. In PRE/F20743, pl. 127(1–3), the number of sporangia ranges from four to seven per cluster, with the sporangia, and most notably the dehiscence lines, radiating out from a receptacle (or common point). The sporangia are preserved, for the most part, with a distinct longitudinal slit that divides the sporangia into two halves (pls 24, 25(1, 2), 127, 128), possibly suggesting that the spores have dehisced. A few specimens, e.g. pl. 128(5, 6) clearly show the characteristic thickened apical cell walls of osmundalean sporangia.
**Birtodites holmesii**

1. PRE/F/10709a pl. 124(1) Holotype

2. PRE/F/10709a pl. 125(1)

3. PRE/F/10709a pl. 125(5, 6)

4. PRE/F/20743 pl. 127(1)

5. PRE/F/12086 pl. 24(4)

6. PRE/F/21103b pl. 25(2)

**Bir 111 (1-3)**

**Aas 411 (4-6)**

- fertile pinna
- adaxial view
- distal annulus
- annulus ray
- dehiscence rib

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**OSMUNDALES**

**Birtodites holmesii**
Birtodites holmesii

Pl. 20

OSMUNDALES
Birtodites holmesii

Birds River
(Bir 111 Sph 2sp)

Holotype
all PRE/F/10709a

x 20
x 10
x 20
x 40
x 20
x 40

1 2 3 4 5

x 20

TF. 4 on p. 74

21 (2008)

OSMUNDALES

pl. 22
Birds River
(Blr 111 Sph 2app)

both BP/2/10709a
Holotype

OSMUNDALES
pl. 23
Birtodites holmesii
Aasvoëlberg
(Aas 411 Dic/Sph)

Birtodites holmesii

Osmundales
Little Switzerland
(Lit 111 Dic/Hei)

Aasvoëlberg
(Aas 411 Dic/Sph)

Osmundales

Birtodites holmesii
Elantodites H.M. And. & J.M. And., gen. nov.

Type species
Elantodites turneri H.M. And. & J.M. And., sp. nov.
Ela 112 Equ sp, Elandspruit (Zorba Stream), Karoo Basin, S. Africa; Carnian, Triassic.

Generic diagnosis
An osmundaceous fern bearing pinnae with a wing-like expanded acroscopic base always present between junction of secondary and tertiary axis; and with fertile pinnules bearing adjacent sporangia covering nearly the entire lamina.

Generic characters
Fertile foliage: frond bipinnate to tripinnafrifid, completely to partly fertile; pinnae and pinnules as for sterile foliage but pinnules usually shorter and more rounded; sporangia closely spaced, small, ca 0.2–0.3 mm diam., attachment sessile, or broadly stalked, circular to broadly oval; annulus distal, asymmetrical, to strongly developed, occupying free surface of sporangium; dehiscence area reduced, of variable length, without prominent ribbed band.

Sterile foliage: frond bipinnate to tripinnatifid; pinnae often elongated, L:W ratio 3–8:1; pinnules entire or lobed to deeply divided, L:W ratio 4–5:1; pinnules of bipinnate forms and pinnate of tripinnate fronds with a wing-like expanded acroscopic base always present between junction of secondary and tertiary axes; venation consisting of elongated well-defined midvein and lateral veins arching or straight and dividing to three times, in acroscopic wing the proximal vein runs parallel to rachis.

Etymology
Elantodites—contrived name; from the type locality Elandspruit and Todites a fossil fern genus similar to the extant Todea.

Global range: 5 spp, Gondwana, Tr (CRN). First & last: the Molteno species described here.

Gondwana Triassic occurrence

Molteno occurrence
Frequency (F): 14 TCs (of the 100 sampled in the Molteno). Diversity (D): 5 species. Abundance (A): 20%–1 indiv., co-dominant to very rare. Habit: unknown, but possibly similar to extant Osmunda, i.e. rhizomatous with numerous fronds. Preferred habitat: common to co-dominant in Heidiphyllum thicket (Ela 112, Pen 221) and Equisetum marsh (Ask 111), and rare in Dicroidium and Sphenobaiera woodland (Bir 111).

Affiliation (fertile & sterile fronds)
Fertile and sterile pinnules occur on the same frond in Elantodites turneri, E. stuartii, E. alisoniae and E. joydeniorum. So far E. kitchingii is known only from totally fertile fronds and the possible affiliated sterile fronds are placed in the genus Parsorphylum. (Consult E. kitchingii for further discussion on a possible Cladophlebus affiliate.) It is interesting to note that the sterile fronds definitely affiliated (based on the fertile specimens) with both E. turneri and E. stuartii are almost identical and, in the absence of fertile material, would both have been placed in the sterile genus Parsorphylum.

Classification & comparison
Suprageneric classification (Osmundaceae/Osmundales)
The diagnostic character for placing Elantodites in the Osmundales and Osmundaceae is the distinct apical band of thickened cells forming an annulus on the sporangia and its dehiscing by a longitudinal slit.

Intergeneric comparison
Nymbopteron, a genus erected by Holmes (2003) for sterile fern-like fronds, has a distinct modified acroscopic pinnule always confluent between the main rachis and pinna rachis (first and second axes of frond) to form a triangular wing. A similar triangular wing occurs in Elantodites but is located between the rachis of the pinna and the first acroscopic pinnule of the secondary pinna (second and third axes of frond).

Parsorphylum Lele (1969) is an Indian genus based on a single ‘bipinnate’ fern-like frond. If it is accepted to be a portion of a tripinnate frond then it has a wing-like pinnule in the same position as Elantodites. No fertile material is known for Parsorphylum from India. Parsorphylum is used for sterile fronds from the Molteno, whereas sterile fronds affiliated with fertile fronds are placed in the new genus Elantodites.

Jain & Delevoryas (1967) illustrated sterile fronds of Cladophlebus meso- zoica (pl. 87; f. 6), C. johnstonii (pl. 87; f. 4, 5) and C. australis (pl. 87; f. 2, 5) which show the presence of a slight wing.

The genus Todites has been widely used in the Gondwana Triassic for ferns with sporangia that are closely spaced and covering the whole lamina surface but of the species described, none appear to show the characteristic acroscopic wing as described here for Elantodites.

Molteno occurrence (elaborated)
The Elantodites species form two groups:
1) Both E. kitchingii and E. turneri occur at Ela 112 (Tab. 6) and may prove to belong to a single species bearing both bipinnate and tripinnatifid fertile fronds, but so far no intermediates occur. At Kon 221 only fertile bipinnate fronds occur, i.e. E. kitchingii, and the possibly affiliated sterile fronds are placed in Parsorphylum.

2) E. joydeniorum, E. stuartii, and E. alisoniae all occur together at Bir 111 and each exhibits distinct features in the distribution of fertile and sterile pinnules on a single pinna/frond.

Gondwana occurrence (elaborated)
A sterile fern described as Gleichenites cachivariensis by Herbst (1996, pl. 1, f. 1, 3) shows a possible wing and similar pinnule venation to Elantodites, but the fertile frond with synangia in groups is quite different. As there is no evidence of attached fertile and sterile foliage, the two fronds described by Herbst may belong to two distinct genera.

Comparisons beyond Gondwana Triassic
Global Mesozoic
The genus Todites includes numerous species worldwide in which fertile pinnules are completely covered in sporangia similar to some of the Molteno fronds described here. The sporangia with thickened cell walls and slits are also similar (see Harris 1961, fig. 29, D, E; 31G). However, we differentiate the Molteno fertile fronds by the presence of the basal acroscopic wing.

Cynepetis, first described from the Chine flora of New Mexico, (Ash 1969, pl. 3, f. 3) has pinnules with scattered sporangia having a similar annulus of thickened cells as in Elantodites. It is also known from the Santa Clara Flora in Mexico (Weber 1985b, f. 1). The sterile pinnules of Cynepetis differ from Elantodites by having all the outer veins anastomosing two or more times.

Extant ferns
The extant genus Todea has similarities to Todites and Elantodites. According to Harris (1961) the sporangia of the living genera Todea and Leptogetheris differ from Todites by the smaller and more laterally located patch of thickened cells (annulus).
Tab. 17. Elantodites, Molteno occurrence

<table>
<thead>
<tr>
<th>Elantodites assemblage (taphocoenosis)</th>
<th>E. turneri (Ela 112)</th>
<th>E. stuartii (Bir 111)</th>
<th>E. alisoniae (Bir 111)</th>
<th>E. kitchingii (Kon 211/221)</th>
<th>E. joydeniorum (Bir 111)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cal 111 Equ sp.</td>
<td>-</td>
<td>-</td>
<td>-</td>
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</tr>
<tr>
<td>Bir 111 Sph 2sp</td>
<td>-</td>
<td>3 50</td>
<td>-</td>
<td>-</td>
<td>-</td>
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<tr>
<td>Cyp 111 Dic cra</td>
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<td>-</td>
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</tr>
<tr>
<td>Kan 112 Hei elo</td>
<td>1 1</td>
<td>-</td>
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</tr>
<tr>
<td>Tel 111 Hei elo</td>
<td>7 44</td>
<td>-</td>
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<tr>
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<tr>
<td>Kra 211 Equ sp</td>
<td>1</td>
<td>-</td>
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<tr>
<td>Kon 223 Dic odo</td>
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<tr>
<td>Kon 211/221 Ast 2sp</td>
<td>-</td>
<td>-</td>
<td>8</td>
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<tr>
<td>Pen 222 Dic/Equ</td>
<td>5 15</td>
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<tr>
<td>Ela 112 Equ sp</td>
<td>18 3</td>
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<tr>
<td>Aas 111 Hei elo</td>
<td>-</td>
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<tr>
<td>Aas 411 Dic/Sph</td>
<td>-</td>
<td>1 1</td>
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<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Ask 111 Equ sp</td>
<td>8 9</td>
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<td>-</td>
</tr>
<tr>
<td>Total TCS</td>
<td>7 5</td>
<td>2 2</td>
<td>1</td>
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<tr>
<td>Total indivs</td>
<td>5 27</td>
<td>4 51</td>
<td>3</td>
<td>28</td>
<td>- 3</td>
</tr>
</tbody>
</table>

Rarity & quality of the fertile Molteno material (Tab. 17)

Of the seven genera of fertile ferns described from the Molteno, Elantodites (as here delineated) is clearly the most diverse (with 5 species), the most frequent (from 14 TCs overall), most abundant (reaching 5% of the TC at Pen 222), and has by far the greatest yield of finely preserved sporangia. It must be reiterated, however, that the overall spread of morphological diversity of the sporangia possibly suggests that Elantodites might in the future warrant splitting into two or three genera; as might E. turneri warrant splitting into two or three species. All the best preserved fertile material for each species is illustrated in the colour plates (pls 129–150).

E. turneri (Ela 112, RP, 18 fertile indivs, pls 129–132). Two of the three specimens illustrated show particularly well-preserved sporangial detail.

E. turneri (3 SPs, Tel 111, Aas 111, Pen 222, pls 133–138). Three of the six available SPs are illustrated here to complement the RP from the Ela 12 TC. Tel 111 and Aas 111 include small fragments with particularly finely preserved sporangia, whilst Pen 222 includes a number of particularly picturesque portions of frond, but only very rarely are there encountered relatively unclearly preserved individual sporangia. No pen sketches of the latter (Pen 222) have been made.

E. stuartii (Bir 111, RP, 3 fertile indivs, pls 139, 140). Whilst the holotype (BP/2/4709, pl. 139) is a fairly complete portion of frond showing clear sporangial arrangement, but no diagnostic detail, the second illustrated specimen (BP/2/4694a, pl. 140), a small fragment judged to belong to the same species, shows sufficient sporangial detail to warrant colour photography and pen sketches.

E. alisoniae (Bir 111, RP, 3 fertile indivs, pls 141–144). The holotype, a large frond fragment, preserves very clear details of the sporangia (thickened annulus cells). The remaining two individuals are of a good deal lesser quality.

E. kitchingii (Kon 211, RP, pls 145, 146). The three specimens (of 8 in the collection) illustrated show the sporangial arrangement well, but the sporangial detail only very faintly.

E. kitchingii (Ela 112, SP, 14 fertile indivs, pls 147–150). Together with E. turneri, with its RP also from Ela 112, this is the best represented and preserved fertile fern species in the Molteno. The three indivs (large portions of frond) selected for colour photography all show finely preserved sporangial detail.

E. joydeniorum (Bir 111, RP). The three fertile indivs of this species are not sufficiently well preserved to merit colour photography.
**Elantodites Elantodites**

- **E. turneri** (1–5) at Ela 112
- **E. stuartii** (6–9) all Bir 111
- **E. joydeniorum** (10) Bir 111

*Elantodites* OSMUNDALES
Elantodites

E. alisoniae (1–3)
al Bir 111

Elantodites

E. kitchingii (4–6)
Kon 221 & Ela 112

OSMUNDALES

Elantodites
Elantodites turneri H.M. And. & J.M. And., sp. nov.

Holotype
Specimen: PRE/F/13240a,b; pls 27, 28, 129, 130.
Assemblage: Ela 112 Equ sp. Elandspruit
Preservation: large portion of tripinnate frond, with counterpart; impression in laminated, grey shale with poor cleavage.

Reference palaeodeme
Specimens: 18 indivs fertile (2 intact, 3 partial, 13 frags); 3% of TC, i.e. 25 indivs sterile (5 intact, 16 partial, 4 frags), pls 27–34, 129–132.

Sister palaeodemes—6
Pen 222 Disc/Equ: 20% of TC (5% fertile, 15% sterile); 14 indivs fertile (2 intact, 3 partial, 9 frags), 46 indivs sterile (3 intact, 9 partial, 34 frags), pls 35, 36, 133, 134.
Tel 111 Hei elo: 7 indivs fertile (1 intact, 6 frags); 44 indivs sterile (7 partial, 37 frags), pls 37, 135, 136.
Aas 111 Equ sp: 12 indivs fertile (frags), pls 137, 138.
Ask 111 Equ sp: 9% of TC, 8 indivs fertile (all frags); 15 indivs sterile (4 intact, 4 partial, 7 frags).
Kra 211 Equ sp: 1 indiv. fertile (frag.).

Specific diagnosis
An Elantodites species with tripinnatifid to tripinnate fronds bearing lanceolate secondary pinnae with fertile pinnules bearing sporangia that commence distally and spread proximally to base of frond.

Specific characters
Fertile foliage: frond tripinnatifid to tripinnate, estimated length 500 mm, fertile distally and waning proximally; pinnules up to 100 mm long, at ca 45° to primary rachis, fertile distally and waning proximally; pinnules lanceolate, pinnatifid, with characteristic triangular wing on acroscopic base, sporangia commence distally and marginally spreading proximally and towards midvein until whole lamina surface covered; sporangia, small, ca 0.2 × 0.25 mm; annulus rays gracile, forking, occasionally meshing; dehiscence area relatively long, faintly irregularly ribbed.
Sterile foliage: frond tripinnatifid to tripinnate, estimated length 500 mm; with characteristic triangular wing on the first acroscopic pinnule of the secondary pinnia; veins forking 1 to 3 times depending on shape and size of pinnule, proximal vein in triangular wing runs parallel to the rachis.

Eponymy
turneri—for Dr Brian Turner, sedimentologist who completed a basin-wide study of the Molteno Fm. in the mid-seventies and who discovered many new localities, including the type locality of this species.

Comment & comparison
Elantodites turneri is distinguished by the distribution of the sporangia which commence from the pinna apex and spread towards the base, in contrast to E. stuartii, E. alisoniae and E. joydeniorum, in which the sporangia spread from the base to the apex. E. joydeniorum is tripinnatifid as in E. turneri. E. kitchingii differs by its bipinnate form.

In the Gondwana Triassic, the sterile fern Nymphopteran foliis Holmes (2003) has similar pinnules but is bipinnate and has a striated main rachis. Todites pattinsoniorum Holmes (1982), T. baldonii (Herbst 1988) and T. parvum (Holmes 2001) have similar fertile pinnules but are bipinnate and do not show the characteristic wing.

No complete fronds have been found. From the type specimen, PRE/F/13240, pl. 27, and others showing a robust rachis, e.g. pl. 33, we estimate a frond length of at least 500 mm. The characteristic wing can be seen in most specimens of both fertile fronds, pls 27(2, 3), 28(3, 4), 30(1), and sterile fronds, pls 33(1, 4), 34(6); see also at Tel 111 and Pen 222, pls 35–37. The commencement of distribution of the sporangia distally and proceeding to the base is well illustrated in specimens from Ela 112, pls 27, 31(1) and Pen 222, pl. 35(5). The lamina is covered with sporangia on specimens shown on pls 29–31(4–7). At Pen 222 there is one unusual specimen with a fertile basal pinnule but otherwise sterile.

Ferns from the type locality can be separated into two groups: fronds tripinnatifid or tripinnate (18 indivs fertile and 25 indivs sterile) being placed in E. turneri, pls 27–34, 129–132; or bipinnate (14 indivs fertile) being placed in E. kitchingii, pls 49, 50, 147–150. We regard these as falling into two populations: although the sporangia in both groups are closely similar, there are no hand specimens that demonstrate intergrading between them. A detached pinnia or isolated pinnule completely covered in sporangia can be difficult to specifically determine.
The Molteno floodplain biome showing the position of the *E. turneri* habitats

References:
Cairncross et al. 1995
And. & And. 2003 (p. 39)

<table>
<thead>
<tr>
<th>Taphocoenoses</th>
<th>Molteno habitats</th>
</tr>
</thead>
<tbody>
<tr>
<td>Kan 112</td>
<td>Hei elo</td>
</tr>
<tr>
<td>Tel 111</td>
<td>*</td>
</tr>
<tr>
<td>Aas 111</td>
<td>*</td>
</tr>
<tr>
<td>Kra 211</td>
<td>Equ sp</td>
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<tr>
<td>Ela 112</td>
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<tr>
<td>Ask 111</td>
<td>*</td>
</tr>
<tr>
<td>Pen 222</td>
<td>Dic/Equ*</td>
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</tbody>
</table>

*Pen 222 Dic/Equ is placed in the *Equisetum* marsh (And. & And. 2003, Tab. 1, p. 4) based on 40% *Equisetum*; but with 40% *Dicroidium*, proximity to the *Dicroidium* woodland habitat is also suggested. The presence of 20% ferns (*E. turneri*) shifts the balance in favour of *Equisetum* marsh.
Elantodites stuartii H.M.And. & J.M.And., sp. nov.

Holotype
Specimen: BP/2/4709; pls 38(1, 6, 7), 139.
Assemblage: Bir 111 Dic/Sph, Birds River.
Preservation: virtually complete pinnae; impression in thinly laminated, yellowish grey shale with very good cleavage.

Reference palaeodeme
Assemblage (TC): as for holotype.
Specimens: 3 indivs fertile (1 partial, 2 frags), ca 50 indivs sterile (intact to frags), pls 38–40, 139, 140.

Sister palaeodeme—1
Aas 411 Hei elo: 1 indiv. fertile (partial); 1 indiv. sterile (partial).

Specific diagnosis
An Elantodites species with bipinnate to tripinnatifid fronds bearing modified fertile pinnules with sporangia that commence from base of proximal pinnules and spread apically and distally.

Specific characters
Fertile foliage: frond bipinnate to tripinnatifid, length unknown, fertile pinnae only known detached; pinnae up to 200 mm long, attachment unknown, fertile proximally and waning distally; sterile pinnae lanceolate, ca 15 × 5 mm, with slight triangular wing on acroscopic base; fertile pinnae modified reduced, rounded lanceolate, ca 6–9 × 4 mm, sporangia commence proximally and along midvein spreading distally and towards margin till whole lamina surface covered; sporangia sessile, ca 0.2 mm diam., annulus gracile, closely reticulate; dehiscence area extends most of sporangial length, with faint elongate cells.

Sterile foliage: frond bipinnate to tripinnatifid to tripinnate; pinnae to 25 mm long and 4 mm wide, with characteristic acroscopic basal wing, margins entire to increasingly lobed and eventually to separate pinnae; lateral veins forking 1 to 3 times depending on shape and size of pinnae, proximal vein in triangular wing runs close and parallel to the rachis.

Eponymy
stuartii—for Stuart Tennent, current owner of the farm Denwood, on which the Birds River locality (Bir 111) occurs. He and his family provided generous assistance and hospitality on our collecting trips.

Comment & comparison
E. stuartii is distinguished by the pinnules becoming fertile basally and in the proximal portion of the pinnae—the reverse of the pattern in E. turneri; E. joydeniorum differs by the longer lobed fertile pinnales; E. alisoniae is bipinnate, with right-angled attachment of the pinnae and entire shorter sterile pinnales.

At Bir 111 this species is well represented, whereas at Aas 411 only two individuals occur. The fertile Aas 411 specimen with pinnales basally fertile and sterile apically is remarkably similar to the type specimen from Bir 111. The sterile frond from Aas 411 also compares closely with the sterile fronds from Bir 111.

At Bir 111 most specimens are isolated pinnales, but one (PRE/F/11814a,b) shows a rachis with four sterile pinnales attached, thus clearly indicating that the fronds are bipinnate to tripinnatifid.
E. stuartii

PRE/F/11814a,b
(not on plates)

BP/2/4694a
pl. 140(3–5)

R2
x 1

BP/2/4709
pl. 139(1)

R2
x 5

BP/2/4694a
pl. 140(3–5)

R2
x 100

all Bir 111

Allium

Elantodites stuartii
Elantodites alisoniae H.M.And. & J.M.And., sp. nov.

Holotype
Specimen: BP/2/4739a,b, pls 41–44, 141–144.
Assemblage: Bir 111 Dic/Sph, Birds River.
Preservation: intact frond, part and counterpart, with 3 pinnae showing fertile and sterile pinnules; impression in thinly laminated, yellowish grey shale with very good cleavage.

Reference palaeodeme
Assemblage (TC): as for holotype.
Specimens: 3 indivs (1 intact, 2 frags), pls 41–44, 141–144.

Sister palaeodemes—nil.

Specific diagnosis
An Elantodites species with bipinnate fronds bearing pinnae with rounded, broadly oblong, proximal fertile pinnules completely covered with sporangia while distal pinnules are sterile.

Specific characters
Fertile foliage: frond bipinnate, to at least 500 mm long, partially fertile; pinnae up to 230 mm long, at ca 90° to primary rachis, fertile proximally; fertile pinnules strongly modified, roundly rhomboid, ca 6 x 7 mm, with slight wing on acroscopic base, sporangia cover whole lamina surface; sterile pinnules roundly lanceolate, at ca 45°–60° from pinna rachis; sporangia closely spaced, medium, ca 0.3 mm diam.; annulus variously asymmetrically arcuate distally, incomplete arcuate proximally, rays irregularly bean-shaped, cells strongly thickened; dehiscence area relatively broad, without ribs.
Sterile foliage: see for sterile pinnules above.

Eponymy
alisoniae—for Alison Tennent (wife of Stuart Tennent) of Denwood Farm, who provided us with a very warm welcome on our collecting trips to the Birds River locality (Bir 111).

Comment & comparison
Elantodites alisoniae is distinguished by fronds bearing fertile pinnules proximally and sterile pinnules distally, whereas E. kitchingii has fertile pinnules on the whole frond. However, isolated fertile pinnules of these two species can look similar. E. alisoniae shares features in common with E. turneri, E. joydeniorum and E. stuartii but has been separated on the basis of being bipinnate, by the right-angled attachment of the pinnae, and the entire, shorter sterile pinnules.

In the arcuate fan of bean-shaped thickened cells (annulus), the sporangia of E. alisoniae appear slightly more reminiscent of Birtodites than the other species of Elantodites. In the shape of its pinnules and arrangement of sporangia, E. alisoniae is very like E. kitchingii. Considering the overall morphology of the species, it falls somewhat between Birtodites and the other species of Elantodites.

The sterile Cladophlebis retallackii (Holmes 2003) has an ‘acroscopically decurrent base’ which is similar to the ‘wing’ in this species, but differs in the lateral venation that arches and forks up to three times.

Elantodites alisoniae is based on the single intact frond showing three lateral pinnae attached to a rachis (pls 41, 42). Although a relatively large fossil block, it shows perhaps only one sixth or even less of the total frond. There is an unfortunate crack in the sediment where some of the pinnules are missing. However, the lateral axis clearly continues across the gap, pl. 41(1, 2). In the part and counterpart, the crack is somewhat out of alignment so that pinnules not seen on one side can be deciphered on the other. See drawing where the crack is indicated by dashed lines. Note that only the pinnules visible on the fossil have been drawn.
**E. alisoniae**

1. Showing only venation, sporangia excluded

2. Pl. 141(2) showing section of f3 between arrows

3. Pl. 143(2)

4. Pl. 144(2)

5. Pl. 144(2)

all BP/24739a
Holotype
Bir 111
Elantodites kitchingii H.M. And. & J.M. And., sp. nov.

Holotype
Specimen: PRE/F/2362a,b, pls 45, 145.
Assemblage: Kon 211/221, Ast 2xpp, Konings Kroon (Rooipoort Donga).
Preservation: intact fertile frond with counterpart, impression in massive light grey shale with poor cleavage.
Note: Kon 211/221 has been selected as the type locality, although Ela 112 has better preserved sporangia. The latter is already the type locality for E. turneri and we feel it better not to make it also the type locality for a species that has such similar sporangia to E. kitchingii.

Reference palaeodeme (RP)
Assemblage (TC): as for holotype.
Specimens: 8 indivs fertile (2 intact, 2 partial, 4 frags); pls 45–48(1–6).

Sister palaeodemes (SPs)—5
Ela 112 Equ sp: 14 indivs fertile (3 intact, 4 partial, 7 frags); pls 49, 50, 147–150.
Kon 223 Dic odo: 1 indiv. fertile (partial); pl. 48(7).
Cal 111 Equ sp: 2 indivs fertile (frags).
Cyp 111 Dic cra: 2 indivs fertile (frags).
Kom 111 Spl/Dic: 1 indiv. fertile (frag.).

Specific diagnosis
An Elantodites species with bipinnate fronds bearing rounded, broadly oblong fertile pinnules with sporangia covering the whole lamina surface.

Specific characters
Fertile foliage: frond bipinnate, estimated up to 300 mm long, fertile throughout; pinnae to >100 mm long, at obtuse angle to primary rachis, fertile throughout; fertile pinnules roundly rhomboid, ca 8 × 6 mm, with triangular wing on acroscopic base, sporangia cover whole lamina surface; sporangia (based on Ela 112 SP) small, 0.25 × 0.3 mm diam.; annulus rays robust, forking, rarely meshing; dehiscence area relatively short, faintly irregularly ribbed.
Sterile foliage: unknown (see notes on affiliation below).

Eponymy
kitchingii— for Dr James Kitching, eminent vertebrate palaeontologist; in appreciation of his practical assistance, especially during the early 1970s at the Bernard Price Institute, University of the Witwatersrand.

Comment & comparison
Elantodites kitchingii is distinguished from the other Molteno species by the completely fertile fronds on which no sterile pinnules are present. The frond is bipinnate and may become slightly tripinnatifid near the base. E. turneri is tripinnatifid to tripinnate and has some sterile pinnules. While individual fertile pinnules may be similar in form, the pinnules are much smaller than in E. kitchingii.

Similar fertile material has been described from South America by Herbst (1988) as Todites baldoni and from Australia by Holmes (1982) as T. pattinsoniorum and T. parvum Holmes (2001), but none of these show the characteristic ‘wing’ as found in Elantodites.

No specimens of E. kitchingii are known with sterile parts in organic attachment to the fertile fronds, so the affiliation of sterile fronds is problematic. Three possibilities arise:

1) At the type locality, Kon 211/221, there are numerous sterile fronds with similar gross morphology to the fertile/sterile fronds of E. turneri, but without attached sporangia. On this basis the sterile fronds from Kon 211 placed in the morph-genus Parsorophyllum (restricted to sterile fronds) may be affiliated. In support of this are the pinnules near the base of PRE/F/10243, pl. 47(1), that tend towards tripinnatifid.

2) A problem is Cladophlebis barbara (17 indivs) which also occurs at Kon 211/221 and could be an affiliate. The pinnules of C. barbara show a slight wing, pl. 70(3), similar to that on the fertile pinnules, pl. 47(7).

3) The totally fertile fronds attributed to E. kitchingii from Ela 112 are associated with cladophlebid fronds (2 individuals which also show the ‘wing’) suggesting Cladophlebis evelynae as an affiliate, (pl. 80). At the other five TCs listed above for E. kitchingii, the pinnule fragments are associated with various Cladophlebis species (see species descriptions and Tab. 6).
**Elantodites joydeniorum** H.M. And. & J.M. And., sp. nov.

**Holotype**
Specimen: PRE/F/4716; pl. 26(1–3).
Assemblage: Bir 111 Dic/Sph, Birds River.
Preservation: intact frond with fertile and sterile pinnules; impression in thinly laminated, yellowish grey shale with very good cleavage.

**Reference palaeodeme**
Assemblage (TC): as for holotype.
Specimens: 3 indivs (2 intact, 1 frag.), pl. 26.

**Sister palaeodemes**—nil.

**Specific diagnosis**
An *Elantodites* species with tripinnatifid fronds bearing lanceolate fertile pinnules with sporangia that commence from base of proximal pinnules and spread irregularly apically and distally.

**Specific characters**
Fertile foliage: frond tripinnatifid, length unknown, fertile proximally and waning distally; pinnae length uncertain; at 45° to primary rachis, fertile proximally and apparently spreading distally; sterile pinnules lanceolate, slightly lobed, 15–20 × 4 mm, at 45°–60° from pinna rachis; fertile pinnules similar to sterile, commence from base of frond and spread distally; sporangia details not preserved.

Sterile foliage: see for sterile pinnules above.

**Eponomy**
*joydeniorum*—for Joy and Den Tennent, owners of the farm Denwood when we first collected from the Birds River (Bir 111) locality in 1970.

**Comment & comparison**
This species is based on two intact individuals and one fragment in which the fronds are mainly sterile. Fertile pinnules are irregular on BP/2/4716, pl. 26(1–3), and appear to be more common on one side of the frond. On BP/2/4740, pl. 26(4, 5), only the base of the proximal pinnules at the lower section of the frond are fertile. This species differs from *E. stuartii* and *E. alisoniae* in the fertile pinnules being tripinnatifid and much longer, while sharing the characteristic acroscopically winged base and similar sporangia. This is close to *E. turneri* in being tripinnatifid but differs in the sporangia commencing from the base and not from the apex of the frond.

Preservation details of sporangia are insufficient for description or comparison with the other four Molteno species of this genus.
Elantodites joydeniorum

Birds River
(Bir 111 Sph 2 spp)
Holotype

Elandspruit
(El 112 Equ sp)
OSMUNDALES

Elantodites turneri

Holotype

Elandspruit
(Ela 112 Equ sp)

x 10

x 2

x 5

x 5
Elantodites turneri

PRE/F/13247a or b (figs 1–6)

Elandspruit
(Ela 112 Equ sp)

PRE/F/13246 (figs 7, 8)

PRE/F/13247a or b (figs 1–6)

PRE/F/13246 (figs 7, 8)
OSMUNDALES

Elantodites turneri

Elandspruit (Ela 112 Equ sp)

All PRE/F13427a or b

Pl. 30

Elantodites turneri
Elantodites turneri
(Ela 112 Equ sp)

BP/2/6408a (figs 1-3)
Elandspruit

PRE/F/13239 (figs 4-7)
Elantodites turneri
(Ela 112 Equ sp)
all PRE/F/13252

Elandspruit
(El 112 Equ sp)
Elantodites turneri

Elandspruit
(Ela 112 Equ sp)
Elantodites turneri

Elandspruit
(Ela 112 Equ sp)

PRE/F/13258 (figs 1, 2)
PRE/F/13238

PRE/F/13260 (figs 4, 5)
PRE/F/6409b (figs 6–8)
Elantodites turneri

PRE/F/14047 (figs 1, 2)

PRE/F/14047b (figs 3, 4)

PRE/F/14076b

Peninsula
(Pen 222 Dic/Equ)
Elantodites turneri

PRE/F/14255 (figs 1, 2)

Peninsula
(Pen 222 Dio/Equ)

PRE/F/14051a (figs 3, 4)

x2  x5

x1
Elantodites turneri

Telemachus Spruit
(Tel 111 Hei eio)
Elantodites stuartii

Birds River
(Bir 111 Sph 2spp)
Elantodites stuartii

Birds River
(Bir 111 Sph 2spp)

specimen missing

Elantodites stuartii pl. 39

OSMUNDALES
Elantodites stuartii

Birds River
(Bir 111 Sph 2spp)

BP/2/4680 (figs 1, 2) x 2
PRE/20180b (figs 3, 4) x 5

Elantodites alisoniae

Birds River
(Bir 111 Sph 2app)

all BP/24739a or b
Holotype

OSMUNDALES
Elantodites alisoniae

Birds River
(Bir 111 Sph 2spp)

all BP2/4739a or b
Holotype
Elantodites alisoniae

Birds River
(Bir 111 Sph 2 spp)

both BP/2/4739a
Holotype
Elantodites kitchingii

Konings Kroon
(Kon 211/221 Ast 2 spp)

all PRE/F/2362a or b

1 x 2
2 x 1
3 x 1
4 x 5
5 x 5
6 x 1
7 x 10
8 x 20
The Brief History of the Gymnosperms

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‘John and Heidi’s ‘Molteno Monographs’, as I have come to call them, represent one of very few current examples of ongoing research with monographic treatment of all the plant fossils in a given geological unit. Indeed, as I write, I am not aware of any other comparable series. The Molteno Monographs are truly remarkable for the in-depth coverage, for their detailed documentation of a fantastic collection of plant fossils and for the sheer hard work and determination shown by the authors over a lifetime devoted to this task. These volumes are, without doubt, the global benchmark for researchers on Triassic floras and, in my judgement, will remain so for many, many generations to come. . . . . I have awaited the fern volume with genuine personal interest as I have had a career-long passion for fossil ferns. . . . . I have not been disappointed.’ Margaret E. Collinson, Professor of Plant Palaeobiology, Royal Holloway University of London (February 2007, from Foreword).

‘My research into fossil plants was initiated by Dr Edna Plumstead during my B.Sc.(Hons) year at the University of the Witwatersrand, Johannesburg. Dr Plumstead was an enthusiastic palaeobotanist and an early proponent of the theory of Continental Drift. But it was Prof. Tom Harris who sparked my interest in fossil fertile ferns during my stay of three months at Reading University where I was studying the techniques of cuticle preparation. . . . . Prof. Harris was well known for his work in the 1930s on the East Greenland fossil floras and was now busy with Volume Four (Ginkgoales & Czekanowskiales) of the Yorkshire Jurassic Flora. He inspired me to describe the Molteno Triassic flora and that has become my lifetime’s work.’ Heidi M. Anderson (from Prefaces).

‘Doing science like doing art is inseparable from the scaffolding of one’s life. Be it the way our brains took in the world in our earliest few years, or the country in which we chance to find ourselves, or who were around at impressionable moments, or whether we break a limb at some inconvenient time, it all shapes our science. It is all there in our Molteno volumes; it is all there in this fern volume. . . . . One recalls Darwin’s reflection that he ended up on the five-year Beagle voyage (“by far the most important event in my life”) as a consequence of the shape of his nose and that his uncle Josiah Wedgwood drove him thirty miles to Shrewsbury (“which few uncles would have done”).’ John M. Anderson (from Prefaces).