



# Proposal to emend the genus *Millerocaulis* Erasmus ex Tidwell 1986 to recombine the genera *Ashicaulis* Tidwell 1994 and *Millerocaulis* Tidwell emend. Tidwell 1994

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**Abstract.** Mesozoic Osmundaceae petrified stems are often referred to the genera *Ashicaulis* Tidwell 1994 or *Millerocaulis* Erasmus ex Tidwell emend. Tidwell 1994, depending only on the presence or absence of leaf gaps in the xylem cylinder. However, this character is problematic for generic distinctions, since some specimens (as in the living Osmundaceae) present or lack these structures, depending on the place where the plant was cut. Furthermore, different authors have identified leaf gaps in some specimens where others reported the absence of these structures. Since this generic separation often leads to incomplete comparisons between the species, it is proposed to combine *Ashicaulis* Tidwell 1994 and *Millerocaulis* Erasmus ex Tidwell emend. Tidwell 1994 in *Millerocaulis* Erasmus ex Tidwell 1986, adding the necessary diagnostic changes.

**Resumen.** PROPUESTA DE ENMIENDA DEL GÉNERO *MILLEROCAULIS* ERASMUS EX TIDWELL 1986 PARA LA RECOMBINACIÓN DE LOS GÉNEROS *ASHICAULIS* TIDWELL 1994 Y *MILLEROCAULIS* ERASMUS EX TIDWELL EMEND. TIDWELL 1994. Los ejes petrificados de Osmundaceae mesozoicas son generalmente referidos a los géneros *Ashicaulis* Tidwell 1994 o *Millerocaulis* Erasmus ex Tidwell emend. Tidwell 1994, dependiendo solo de la presencia o ausencia de lagunas foliares en el cilindro de xilema. Sin embargo, este carácter resulta problemático para realizar distinciones genéricas, dado que algunos especímenes (como en las Osmundaceae vivientes) presentan o carecen de estas estructuras, dependiendo del lugar en donde la planta fue cortada. Además, diferentes autores han identificado lagunas foliares en algunos especímenes donde otros informaron la ausencia de estas estructuras. Dado que esta separación genérica en general lleva en general a comparaciones incompletas entre las especies, se propone combinar *Ashicaulis* Tidwell 1994 y *Millerocaulis* Erasmus ex Tidwell emend. Tidwell 1994 en *Millerocaulis* Erasmus ex Tidwell 1986, agregando los cambios necesarios en la diagnosis.

**Key words.** *Millerocaulis*, *Ashicaulis*, Osmundaceae, systematics, Osmundales.

**Palabras clave.** *Millerocaulis*, *Ashicaulis*, Osmundaceae, sistemática, Osmundales.

## Introduction

In 1967, Miller proposed the informal “*Osmundacaulis herbstii* group”, suggesting that it could be considered a natural group included in the morphogenus *Osmundacaulis* Miller. This group received the generic name *Millerocaulis* in Erasmus unpublished doctoral dissertation (1978), but was formally validated by Tidwell (1986). Posteriorly, Hill *et al.* published a new osmundalean fossil genus, *Australosmunda*, which closely resembled *Millerocaulis* Erasmus ex Tidwell, but lacking leaf gaps in the xylem cylinder. But, as noticed by Tidwell (1994), several species of *Millerocaulis* Erasmus ex Tidwell (including its type, *M. dunlopiae* Kidston et Gwynne-

Vaughan) lack (or present occasionally) definite leaf gaps. Thus, he retained the generic name for “true” siphonostelic (having siphonosteles without leaf gaps) species of the genus, and proposed the new genus *Ashicaulis* Tidwell for the species formerly present in *Millerocaulis* with many definite leaf gaps. Furthermore, *Australosmunda* Hill, Forsyth *et Green* (1989), was proposed as a junior synonym of *Millerocaulis*. These two morphogenera have been widely used, and more than 25 species of *Ashicaulis* and nearly ten of *Millerocaulis* are recognized, all of them recorded worldwide in Mesozoic sediments.

Recently, the utility of the morphogenus *Ashicaulis* was questioned by Herbst (2001, 2006), who suggested that *Ashicaulis* and *Millerocaulis* separation is based on a very weak character, which can be present and absent in the same taxon. Furthermore, he pointed out that, depending on the author, one same species (or even a specimen) can be described with or without leaf gaps.

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In this work, the validity of the morphogenus *Ashicaulis* Tidwell is discussed, and the combination of it to *Millerocaulis* Erasmus ex Tidwell is proposed, adding the necessary diagnostic changes to the latter morphogenus.

## Systematic palaeontology

### Order OSMUNDALES

Family OSMUNDACEAE *sensu* Tidwell et Parker, 1987  
Subfamily OSMUNDOIDEA Miller *emend.* Tidwell et Parker, 1987

*Millerocaulis* Erasmus ex Tidwell, 1986 non 1994, *emend.* Vera

**Emended diagnosis.** Fossil osmundaceous rhizomes, rarely arborescent axes, containing stem or stems surrounded by a mantle of leaf bases and roots. Stele either simple ectophloic siphonostele or ectophloic dictyoxyllic-siphonostele (Miller, 1971) with a xylem cylinder approximately 15 tracheids thick. Leaf trace separates from the xylem cylinder with only one protoxylem cluster and often, but not always, lacks axillary sclerenchyma. Petiole bases stipulate and adventitious roots arise either singly or in pairs.

**Type species.** *M. dunlopii* (Kidston et Gwynne-Vaughan) Tidwell, 1986.

*Millerocaulis australis* (Vera) Vera, comb. nov.

2007. *Ashicaulis australis* Vera, Cretaceous Research 28: 501. figures 2-5. Diagnosis, holotype, locality and other data, as in Vera 2007.

*Millerocaulis livingstonensis* (Cantrill) Vera, comb. nov.

1997. *Ashicaulis livingstonensis* Cantrill, New Zealand Journal of Geology and Geophysics 40: 317. figures 2-5. Diagnosis, holotype, locality and other data, as in Cantrill 1997.

*Millerocaulis macromedullosus* (Matsumoto et al.) Vera, comb. nov.

2006. *Ashicaulis macromedullosus* Matsumoto, Saiki, Zhang, Zheng and Wang, Paleontological Research 10: 196. figures 2-5. Diagnosis, holotype, locality and other data, as in Matsumoto et al. 2006.

*Millerocaulis woolfei* (Rothwell et al.) Vera, comb. nov.

2002. *Ashicaulis woolfei* Rothwell, Taylor and Taylor. American Journal of Botany 89: 353. figures 1-18. Diagnosis, holotype, locality and other data, as in Rothwell et al. 2002.

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*Millerocaulis amajolensis* (Sharma) Tidwell.

1973. *Osmundacaulis amajolensis* Sharma, Palaeontographica 140B: 156.  
1986. *Millerocaulis amajolensis* (Sharma) Tidwell, Sida 11: 402.  
1994. *Ashicaulis amajolensis* (Sharma) Tidwell, Sida 16: 256.

*Millerocaulis beardmorensis* (Schopf) Tidwell.

1978. *Osmundacaulis beardmorensis* Schopf, Canadian Journal of Botany 56: 3034.  
1986. *Millerocaulis beardmorensis* (Schopf) Tidwell, Sida 11: 402..  
1994. *Ashicaulis beardmorensis* (Schopf) Tidwell, Sida 16: 256.

*Millerocaulis broganii* Tidwell, Munzing et Banks

1991. *Millerocaulis broganii* Tidwell, Munzing et Banks, Palaeontographica 223B: 98.  
1994. *Ashicaulis broganii* (Tidwell, Munzing et Banks) Tidwell, Sida 16: 256.

*Millerocaulis chubutensis* (Herbst) Tidwell

1977. *Osmundacaulis chubutensis* Herbst, Facena 1:25.  
1994. *Millerocaulis chubutensis* (Herbst) Tidwell, Sida 16: 225.

*Millerocaulis donponii* Tidwell et Clifford

1995. *Millerocaulis donponii* Tidwell et Clifford, Australian Systematic Botany 8: 674.

*Millerocaulis dunlopii* (Kidston et Gwynne-Vaughan) Tidwell

1907. *Osmundites dunlopii* Kidston et Gwynne-Vaughan, Transactions of the Royal Society of Edinburgh 45(1): 759. ("dunlopi").  
1924. *Osmundites aucklandicus* Marshall, Transactions and Proceedings of the New Zealand Institute. 56: 210.  
1971. *Osmundacaulis dunlopii* (Kidston et Gwynne-Vaughan) Miller. Contributions to the Museum of Paleontology University of Michigan (21:146. 1967 ("dunlopi"), nom. invalid. under Art. 33.2- no page reference for basionym) 23:135.  
1986. *Millerocaulis dunlopii* (Kidston et Gwynne-Vaughan) Tidwell, Sida 11: 402.  
1994. *Millerocaulis dunlopii* (Kidston et Gwynne-Vaughan) Tidwell, Sida 16: 255.

*Millerocaulis embreei* Stockey et Smith

2000. *Millerocaulis embreei* Stockey et Smith, International Journal of Plant Sciences 161: 160.

*Millerocaulis estipularis* (Sharma et al.) Tidwell

1979. *Osmundacaulis estipularis* Sharma, Bohra et Singh, Phytomorphology 29: 46. ("estipulare").  
1986. *Millerocaulis estipularis* (Sharma, Bohra et Singh) Tidwell, Sida 11: 403.  
1994. *Ashicaulis estipularis* (Sharma, Bohra et Singh) Tidwell, Sida 16: 256.

*Millerocaulis gibbiana* (Kidston et Gwynne-Vaughan) Tidwell

1907. *Osmundites gibbiana* Kidston et Gwynne-Vaughan, Transactions of the Royal Society of Edinburgh 45: 763.  
 1971. *Osmundacaulis gibbiana* (Kidston et Gwynne-Vaughan) Miller, Contributions to the Museum of Paleontology University of Michigan (21: 146. 1967, nom. invalid under Art. 33.2 - no page reference for basionym) 23: 136.  
 1986. *Millerocaulis gibbiana* (Kidston et Gwynne-Vaughan) Tidwell, Sida 11: 403.  
 1994. *Ashicaulis gibbiana* (Kidston et Gwynne-Vaughan) Tidwell, Sida 16: 256.

### *Millerocaulis guptai* (Sharma) Tidwell

1973. *Osmundacaulis guptai* Sharma, Palaeontographica 140B: 154.  
 1986. *Millerocaulis guptai* (Sharma) Tidwell, Sida 11: 403.  
 1994. *Ashicaulis guptai* (Sharma) Tidwell, Sida 16: 256.

### *Millerocaulis hebeiensis* (Wang) Tidwell

1983. *Osmundacaulis hebeiensis* Wang, Review of Paleobotany and Palynology 39: 93.  
 1986. *Millerocaulis hebeiensis* (Wang) Tidwell, Sida 11: 403.  
 1994. *Ashicaulis hebeiensis* (Wang) Tidwell, Sida 16: 256.

### *Millerocaulis herbstii* (Archangelsky et de la Sota) Tidwell

1963. *Osmundites herbstii* Archangelsky et de la Sota, Ameghiniana 3: 135.  
 1971. *Osmundacaulis herbstii* (Archangelsky et de la Sota) Miller, Contributions to the Museum of Paleontology University of Michigan (21: 146. 1967, nom. invalid under Art. 33.2 - no page reference for basionym) 23: 134.  
 1986. *Millerocaulis herbstii* (Archangelsky et de la Sota) Tidwell, Sida 11: 403.  
 1994. *Ashicaulis herbstii* (Archangelsky et de la Sota) Tidwell, Sida 16: 256.

### *Millerocaulis indentata* (Hill, Forsyth et Green) Tidwell

1989. *Australosmunda indentata* Hill, Forsyth et Green, Palaeontology 32: 292.  
 1994. *Millerocaulis indentata* (Hill, Forsyth et Green) Tidwell, Sida 16: 225.

### *Millerocaulis indica* (Sharma) Tidwell

1973. *Osmundacaulis indica* Sharma, Palaeontographica 140B: 157.  
 1986. *Millerocaulis indica* (Sharma) Tidwell, Sida 11: 403.  
 1994. *Millerocaulis indica* (Sharma) Tidwell, Sida 16: 255.

### *Millerocaulis johnstonii* Tidwell, Munzing et Banks

1991. *Millerocaulis johnstonii* Tidwell, Munzing et Banks, Palaeontographica 223B: 94.  
 1994. *Millerocaulis johnstonii* (Tidwell, Munzing et Banks) Tidwell, Sida 16: 256.

### *Millerocaulis juandahensis* Tidwell et Clifford

1995. *Millerocaulis juandahensis* Tidwell et Clifford, Australian Systematic Botany 8: 669.

### *Millerocaulis kidstonii* (Stopes) Tidwell

1921. *Osmundites kidstonii* Stopes, Annals of Botany 35: 55. ("kidstonii").  
 1971. *Osmundacaulis kidstonii* (Stopes) Miller, Contributions to the Museum of Paleontology University of Michigan (21: 146. 1967 ("kidstonii"), nom. invalid under Art. 33.2 - no page reference for basionym) 23: 136.  
 1986. *Millerocaulis kidstonii* (Stopes) Tidwell, Sida 11: 403.  
 1994. *Ashicaulis kidstonii* (Stopes) Tidwell, Sida 16: 256.

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1907. *Osmundites kolbei* Seward, Geological Magazine, n.s. 4: 482.  
 1971. *Osmundacaulis kolbei* (Seward) Miller, Contributions to the Museum of Paleontology University of Michigan (21: 146. 1967, nom. invalid under Art. 33.2 - no page reference for basionym) 23: 136.  
 1986. *Millerocaulis kolbei* (Seward) Tidwell, Sida 11: 403.  
 1994. *Ashicaulis kolbei* (Seward) Tidwell, Sida 16: 256.

### *Millerocaulis liaoningensis* Zhang et Zheng

1991. *Millerocaulis liaoningensis* Zhang et Zheng, Acta Paleontologica Sinica 30: 717.  
 1994. *Ashicaulis liaoningensis* (Zhang et Zheng) Tidwell, Sida 16: 256.

### *Millerocaulis limewoodensis* Tidwell et Clifford

1995. *Millerocaulis limewoodensis* Tidwell et Clifford, Australian Systematic Botany 8: 677.

### *Millerocaulis lutzi* (Herbst) Herbst

1994. *Maraya lutzi* Herbst, Acta Geologica Leopoldensia 17: 95.  
 2006. *Millerocaulis lutzi* (Herbst) Herbst, Revista del Museo Argentino de Ciencias Naturales 8: 186.

### *Millerocaulis patagonica* (Archangelsky et de la Sota) Tidwell

1962. *Osmundites patagonica* Archangelsky et de la Sota, Ameghiniana 2: 153.  
 1971. *Osmundacaulis patagonica* (Archangelsky et de la Sota) Miller, Contributions to the Museum of Paleontology University of Michigan (21: 146. 1967, nom. invalid under Art. 33.2 - no page reference for basionym) 23: 136.  
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 1994. *Ashicaulis patagonica* (Archangelsky et de la Sota) Tidwell, Sida 16: 257.

### *Millerocaulis preosmunda* Cheng, Wang et Li

2007. *Millerocaulis preosmunda* Cheng, Wang et Li, International Journal of Plant Sciences 168: 1352.

### *Millerocaulis rajmahalensis* (Gupta) Tidwell

1968. *Osmundites rajmahalensis* Gupta, Proceedings of the India Science Congress, Varanasi, 55: 428.  
 1970. *Osmundites rajmahalensis* Gupta, Palaeontographica 130B: 174.

1973. *Osmundacaulis rajmahalensis* (Gupta) Sharma, Palaeontographica 140B: 152.  
 1986. *Millerocaulis rajmahalensis* (Gupta) Tidwell, Sida 11: 403.  
 1994. *Ashicaulis rajmahalensis* (Gupta) Tidwell, Sida 16: 257.

#### *Millerocaulis richmondii* Tidwell

1992. *Millerocaulis richmondii* Tidwell, Papers and Proceedings of the Royal Society of Tasmania 126: 1-2.  
 1994. *Ashicaulis richmondii* (Tidwell) Tidwell, Sida 16: 257.

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1955. *Osmundites sahnii* Mitre, Palaeobotanist 4: 113.  
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 1986. *Millerocaulis sahnii* (Mitre) Tidwell, Sida 11: 403.  
 1994. *Ashicaulis sahnii* (Mitre) Tidwell, Sida 16: 257.

#### *Millerocaulis santaecrucis* (Herbst) Herbst

1977. *Osmundacaulis santaecrucis* Herbst. Facena 1: 21.  
 1994. *Ashicaulis santaecrucis* (Herbst) Tidwell. Sida 16: 257.  
 1995. *Millerocaulis santaecrucis* (Herbst) Herbst. Mededelingen Rijks Geologische Dienst 53: 16.

#### *Millerocaulis sinica* Cheng et Li

2007. *Millerocaulis sinica* Cheng et Li. Review of Paleobotany and Palynology 144: 253.

#### *Millerocaulis spinskii* Tidwell, Munzing et Banks

1991. *Millerocaulis spinskii* Tidwell, Munzing et Banks, Palaeontographica 223B: 96.  
 1994. *Ashicaulis spinskii* (Tidwell, Munzing et Banks) Tidwell, Sida 16: 257.

#### *Millerocaulis stipabonetti* Herbst

1995. *Millerocaulis stipabonetti* Herbst, Mededelingen Rijks Geologische Dienst 53: 15.

#### *Millerocaulis swanensis*. Tidwell, Munzing et Banks

1991. *Millerocaulis swanensis*. Tidwell, Munzing et Banks, Palaeontographica 223B: 99.  
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1970. *Osmundacaulis wadei* Tidwell et Rushforth, Bulletin of the Torrey Botanical Club 97: 137.  
 1986. *Millerocaulis wadei* (Tidwell et Rushforth) Tidwell, Sida 11: 403.  
 1994. *Ashicaulis wadei* (Tidwell et Rushforth) Tidwell, Sida 16: 257.

#### *Millerocaulis websteri* Tidwell, Munzing et Banks

1991. *Millerocaulis websteri* Tidwell, Munzing et Banks, Palaeontographica 223B: 97.

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1994. *Ashicaulis websteri* (Tidwell, Munzing et Banks) Tidwell, Sida 16: 257.

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1991. *Millerocaulis wrightii* Tidwell, Munzing et Banks, Palaeontographica 223B: 93.  
 1994. *Ashicaulis wrightii* (Tidwell, Munzing et Banks) Tidwell, Sida 16: 257.

## Discussion

The genus *Ashicaulis* was proposed in 1994 and, after that, several species of Mesozoic Osmundalean rhizomes were included in it, or in the emended genus *Millerocaulis*. In most of the works dealing with new species of both genera, the methodology followed for comparisons was almost the same. First, the presence or absence of leaf gaps (or incipient leaf gaps) determined the genus (*Millerocaulis* or *Ashicaulis*), and then intrageneric comparisons were made (for determining if it was a new species or a previously described one). It has been demonstrated that several osmundalean species present and lack leaf gaps in transverse section, depending on the level of the plant or the degree of ontogenetic development. For example, Herbst (1994) proposed the osmundaceous morphogenus *Maraya* for including two specimens recovered from Triassic strata of the San Juan province (Argentina), interpreted as true siphonostelic, and assigned it to the sub-family Thamnopteroidea. A later collection of more specimens from the same locality (Marayes) allowed a new analysis of the taxon, and since several of them showed narrow leaf gaps in its xylem cylinder, it was re-interpreted by Herbst as possible different ontogenetic stages of a typical *Millerocaulis* Erasmus ex Tidwell stem (Herbst, 2006). Presence and absence of leaf gaps in the same taxon was also recorded for *Palaeosmunda williamsii* Gould (and probably *P. playfordii* Gould) (Gould, 1970) and for the extant species *Leptopteris superba* (Colenso) C. Presl, where the basal part of the plant presents a protostelic stele, changing its shape to a siphonostelic stele without leaf gaps, and finally becoming an ectophloic dictyoxyllic-siphonostele (Hewitson, 1962: figure 10.K). Hewitson (1962) also noticed that in branching regions of the plant, leaf trace may depart without leaving a leaf gap, and Cantrill (1997) observed some leaf traces of *Ashicaulis livingstonensis* departing from the stele without the presence of a leaf gap. Furthermore, Miller (1971), when describing *Millerocaulis dunlopiae*, pointed out: "The near absence of leaf-gaps in the type specimen is not typical for the species. In all instances, leaf-gaps are very narrow, but they are generally present with most of them incompletely

formed. Leaf-gaps are more distinct in other specimens of this species" (Miller, 1971: 136). This author also included *Osmundites aucklandicus* Marshall (1924) in *Osmundacaulis dunlopii* (now *Millerocaulis dunlopii*), presenting the former species well defined narrow leaf gaps. It is interesting to note that this synonymy was followed as valid by Tidwell (1994) when he defined the type species of the gapless genus *Millerocaulis* Erasmus ex Tidwell *emend.* Tidwell.

On the other hand, discrepancies between authors are present regarding the state of this character. For example, Herbst (1977) described *Osmundacaulis chubutensis* Herbst (now *Millerocaulis chubutensis*) as presenting narrow and not-immediate leaf gaps, whereas Tidwell (1994) illustrated it as lacking leaf gaps, opinion later rejected by Herbst (2006). It is important to point out that the photographs of the type specimen of *Millerocaulis chubutensis* illustrated by Herbst (1977) clearly show the presence of narrow leaf gaps (Herbst, 1977. Plate 3, figures. 34, 35.). *Millerocaulis indica* (Sharma) Tidwell, also considered by Tidwell as lacking leaf gaps, was originally described by Sharma (1973) as "...the leaf gap closes before the trace breaks away and hence the gap is not evident in a single transverse section..." (Sharma, 1973: 157) suggesting that it presents leaf gaps that are difficult to see if only one transverse section is used. Furthermore, Herbst (2001) proposed to consider the four species described by Sharma (1973) (*Millerocaulis indica*, *M. gupta*, *M. amajolensis*, *M. rajmahalensis*) as a single taxon (hypothesis derived after the study of the changing stelar morphology of *Millerocaulis patagonica*), resulting in a single species with differences in the characteristics of the leaf gaps, depending on the ontogenetic stage.

Finally, the most important problem with using these two morphotaxa is related to the criteria followed for the distinction between species: new specimens assigned to *Ashicaulis* should be compared with previously described species for *Ashicaulis* and *Millerocaulis*, with the same being valid for new *Millerocaulis* species. Unfortunately, after the proposal of the new genus *Ashicaulis*, almost every new taxon described as *Millerocaulis* was not compared with any *Ashicaulis* species (Stockey and Smith, 2000; Cheng and Li, 2007; Cheng, Wang and Li, 2007), and no new *Ashicaulis* was compared with the previously known *Millerocaulis* species (Cantrill, 1997; Rothwell *et al.*, 2002; Matsumoto *et al.*, 2006; Vera, 2007). It is noteworthy that evolutionary trends or migration patterns have been proposed for this group of plants, with *Ashicaulis* and *Millerocaulis* evaluated as if they were two different biological entities (*i.e.* Matsumoto *et al.*, 2006). However, only Herbst (1995, 2001, 2006), considers *Ashicaulis* as a biologically non-valid taxon

and continued using *Millerocaulis sensu* Tidwell 1986, and Tidwell and Clifford (1995), and made "intergeneric" comparisons between his specimens and the species included in both *Ashicaulis* and *Millerocaulis*.

## Conclusions

The proposal to split *Millerocaulis* Erasmus ex Tidwell in several morphogenera may be adequate, but it is clear that a separation based only in the presence or absence of leaf gaps is misleading. First, the "intergradation" between species of *Millerocaulis* and *Ashicaulis* makes this separation difficult, and some species can have leaf gaps in certain sections of a plant, being gapless in the rest of the same plant. Furthermore, several species have been described as having or lacking these structures, depending on the author. On the other hand, evidence from living (and fossil) representatives of the Osmundaceae show that at least some species change the morphology of the stele during ontogeny, lacking leaf gaps in the earlier-formed siphonostele, and later developing the ectophloic dictyoxyllic-siphonostele. Finally, these two morphogenera have been treated as if they were real biological entities, including one genus and excluding the other in specific comparisons and phytogeographical discussions, leading to results that may be modified or supported if all the species of both morphogenera were included in the analysis.

In conclusion, the genus *Ashicaulis* is considered here uninformative and misleading, and the conservative use of *Millerocaulis* Erasmus ex Tidwell is proposed, adding necessary diagnostic changes. The discovery of new specimens of this family of ferns will probably lead to better systematic classification, allowing a more natural separation between morphotaxa.

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