**BIODIVERSITAS**
Volume 11, Number 1, January 2010
Pages: 9-14

ISSN: 1412-033X (printed edition)
ISSN: 2085-4722 (electronic)
DOI: 10.13057/biodiv/d110103

# Systematic studies of Australian stipoid grasses (*Austrostipa*) based on micro-morphological and molecular characteristics

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Manuscript received: 25 October 2009. Revision accepted: 26 December 2009.

## ABSTRACT

*Bustam BM (2010) Systematic studies of Australian stipoid grasses (*Austrostipa*) based on micro-morphological and molecular characteristics. Biodiversitas 11: 9-14.* This research is one of many studies on stipoid grasses organized by the International Stipeae Working Group (ISWG). This research tested the subgeneric classification of *Austrostipa* proposed by Jacobs and Everett (1996) and tested how informative the micro morphological characters used. Data were collected from herbarium specimens of 36 species (33 species of *Austrostipa*, two species of *Hesperostipa* and one species of *Anemanthele*) at Royal Botanic Gardens, Sydney. Twenty eight micro morphological characters were used. The data were collected from both adaxial and abaxial surfaces of leaves, and from the lemma epidermis using a scanning electron microscope (SEM). ISWG provided the molecular data. Parsimony analysis and a distance method (Unweighteic Pair Group with Arithmatic Mean: UPGMA) were used to analyze micro-morphological and molecular data separately. Only UPGMA analysis was used to analyze the combined data. The results support the monophyly of *Austrostipa*. However, there is a little support for the subgeneric classification of *Austrostipa* proposed by Jacobs and Everett (1996), other than for the consistent recognition of *Falcatae.* The characters for comparisons between genera are too homoplasious at this level and do not contain enough information for analyses at subgeneric level, a problem apparently shared with the DNA sequences.

**Key words:** *Austrostipa,* stipoid grasses, micro morphological, molecular

## INTRODUCTION

The tribe *Stipeae* was first formulated by Dumortier in 1823, based on the genus *Stipa* L. English names applied to the tribe include Speargrass, Feathergrass and Needlegrass (Townrow 1978). This is a cosmopolitan tribe comprising approximately 500 species (Barkworth 1993). These grasses grow in temperate Australia, North and South America, Europe and Central Asia (Barkworth and Everett 1986; Hsiao et al. 1999). This tribe has been variously placed. The treatment most widely accepted at present is to regard the Stipeae as a tribe of the subfamily Pooideae (Hsiao et al. 1999; Jacobs et al. 2000; GPWG 2000; Wheeler et al. 2002). At present, the relationships within the stipoid grasses are poorly understood, with different data sets suggesting different relationships (Ariaga and Barkworth 2000; Cialdella and Giussani 2002; Connor and Edgar 2002; Maze et al. 2002; Vasques and Barkworth 2004; Ariaga and Barkworth 2006; Ariaga and Jacobs 2006; Barkworth et al. 2008). Understanding the relationships of these grasses allows more effective and efficient resource management (Garden et al. 2000; Clarke 2003; Landberg et al. 2003; de Lange et al. 2004; Huxtable et al. 2005).

Bentham (1878) was the first person to provide treatment of Australian species of *Stipa.* After that, some studies have been conducted to get better understanding of those Australian species of *Stipa* (Hughes 1921, 1922; Everett and Jacobs 1983; Barkworth and Everett 1987; Vickery et al. 1986; Everett 1990; Jacobs and Everett 1996). Based on those studies and the fact that Australian species are more closely related to each other than to any non-Australian species, Jacobs and Everett (1996) decided the best option was to place all the Australian species formerly included in *Stipa* in a new genus, *Austrostipa.*

However, the relationships among subgenera in *Austrostipa* still need to be tested. Jacobs et al. (2000) have DNA sequences for several species. While these DNA sequences strongly supported some groupings or sub genera, other groupings were either poorly supported or not supported at all. The most reliable way of testing any data set would be to compile other data sets based on different characters and look for corroboration. In an attempt to find the relationships of the subgenera within genus *Austrostipa*, it was decided to compile micro morphological data sets for comparison with DNA sequences.

The objectives of this study were: (i) testing whether the subgenera in *Austrostipa* are natural or monophyletic groups, (ii) how informative the micro morphological characters are. This study was conducted at Royal Botanic Gardens, Sydney, Australia, from August 2002 to March 2006.

## MATERIALS AND METHODS

All micro morphological data were collected from herbarium specimens of 36 species (33 species of *Austrostipa*, two species of *Hesperostipa* and one species

of *Anemanthele*). Data were collected from leaves and lemma. Leaves are elongated structures made up of a basal cylindrical sheath and an upper blade or lamina. For this study, only the blade (lamina) of the leaf was used. The lamina was cut approximately 4 cm from the blade/sheath junction and, for both abaxial and adaxial surfaces; a segment of approximately 3 mm of both abaxial and adaxial surfaces was taken for examination. The lemma is the outer bract subtending the floret and is on the side of the spikelet axis away from the main inflorescence axis (Wheeler et al. 2002). For every species, approximately six lemmas were taken, particularly those that were mature and loose from the glumes. Micro morphological data were collected using a Cambridge S360 Scanning Electron Microscope (SEM). Theoretically, all specimens were examined with the same magnification. However, due to different structures of each specimen, the magnification is changed to suit the specimens. All micro morphological characters were scored. In determining the scoring characters, the suggestions of Ellis (1979) were followed, except for the stomata and subsidiary cell size characters, where the scoring was based on the result of preliminary analyses.

The parameters of micro morphological data were:

A. Leaf epidermis characters (adaxial and abaxial surfaces)
1. Difference over (costal) and between veins (intercostal): 0 - absent (the costal and intercostals areas are indistinguishable); 1 - present (the costal and intercostals areas are distinguishable)
2. Silica bodies presence: 0 - absent ; 1 - present
3. Longitudinal cell wall: 0 - smooth; 1 - sinuous
4. Stomata abundance: 0 - few stomata = < 10 stomata per unit area exposed on the SEM (magnification of 200x); 1 - sinuous = ≥ 10 stomata per unit area exposed on the SEM (magnification of 200x).
5. Stomata size, this character measured the length of guard cell approximately (µm): 0 - (≤ 20); 1- (>20 - 23); 2 - (>23 - 26); 3 - (>26 - 29); 4 - (>29 - 32); 5 - (>32 - 35); 6 - (>35).
6. Stomata subsidiary cell size: The scoring is the same as in stomata size (µm)
7. Stomatal shape: 0 - dome-shaped; 1 - parallel sided
8. Macrohairs presence: 0 - absent; 1 - present
9. Macrohairs position: - missing (inapplicable); 0 - both in costal and intercostals areas; 1 - in costal areas only; 2 - in intercostal areas only
10. Prickles presence: 0 - absent; 1 - present
11. Prickles position: - missing (inapplicable); 0 - both in costal and intercostals areas; 1 - in costal areas only; 2 - in intercostal areas only

B. Lemma characters of fundamental cells
12. Length of fundamental cells compared to short cells: - inapplicable; 0 - fundamental cells longer than short cells; 2 - fundamental cells shorther than short cells
13. Sidewall shape: 0 - straight; 1 - wavy; 2 - dentate
14. Sidewall thickness: 1 - not conspicuously thickened; 2 - conspicuously thickened
15. Endwall shape: 1 - straight; 2 - wavy
16. Short cells hooks presence: 0 - absent; 1 - present
17. Lemma silica bodies: 0 - absent; 1 - present

There were 28 micro morphological characters used in this research, 22 characters from leaves (eleven characters for abaxial and eleven characters for adaxial) and six characters for lemmas. Sequences for the ITS region (molecular data) were obtained for the same taxa. The ITS sequences were done by Dr. Randall Bayer, a member of International Stipeae Working Group (ISWG) from Australia, and Dr. Catherine Hsaio from USDA, Longan. All data, micro morphological and molecular were entered into a computer programmed MacClade 4.05 (Madison and Madison 2002) and were then analyzed with PAUP (Phylogenetic Analysis Using Parsimony) version 4.0b10 (Swofford 2002). Parsimony analysis and a distance method (Unweighted Pair Group with Arithmetic Mean: UPGMA) were used to analyze micro morphological and molecular data separately. However only UPGMA analysis was used to analyze the combined data, since preliminary analyses of separated data retrieved some similar groups.

## RESULTS AND DISCUSSION

*Micro morphological analyses*

There are several groups resolved from the micro morphological analyses in both parsimony and UPGMA. However, most of the groups have no bootstrap support and have no support from the molecular analyses. In addition, most of the groups are not the same as groups in recent classification of *Austrostipa* by Jacobs and Everett (1996). For example, the group consisting of three species: *Austrostipa acrociliata*, *A. bigeniculata* and *A. aristiglumis* retrieved in the parsimony analysis of micro morphological data (Figure 1), were placed in two groups in the recent classification (Jacobs and Everett 1996). *A. acrociliata* is in subgenus *Arbuscula* whereas *A. bigeniculata* and *A. aristiglumis* are in subgenus *Ceres*. However, the analysis placed *A. acrociliata* together with *A. bigeniculata* rather than *A. bigeniculata* with *A. aristiglumis*.

Morphologically, there are many similarities between *A. bigeniculata* and *A. aristiglumis*. For instance, both species have open and spreading panicles and non-branching culms. Both *A. bigeniculata* and *A. aristiglumis* have a lemma with a coma, non-tuberculate surface and a short strongly-angled callus while *A. acrociliata* does not have a coma and the lemma has a tuberculate surface and a blunt callus.

There are two groups retrieved from the micro morphological analyses that are consistent with the subgenera in the recent classification by Jacobs and Everett (1996). The first group is retrieved from the parsimony analysis (Figure 1) and consists of two species: *A. nitida* and *A. nodosa*. This group is also retrieved in the UPGMA analysis of micro morphological data (Figure 3), with the addition of one species, *A. scabra* subsp. *falcata*. All three species: *A. nitida*, *A. nodosa*, *A. scabra* subsp. *falcata* are placed in subgenus *Falcatae* in Jacobs and Everett (1996). The other group that is retrieved in the UPGMA analysis of micro morphological data (Figure 3) consists of two species: *A. geoffreyi* and *A. juncifolia*, which placed in subgenus *Lobatae* (Jacobs and Everett 1996). While there

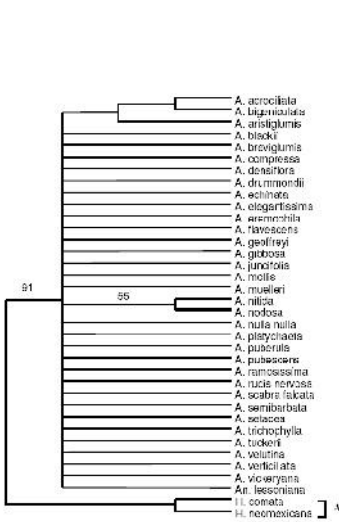


**Figure 1**

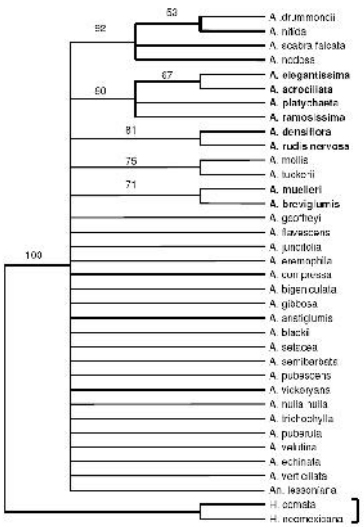


**Figure 2**

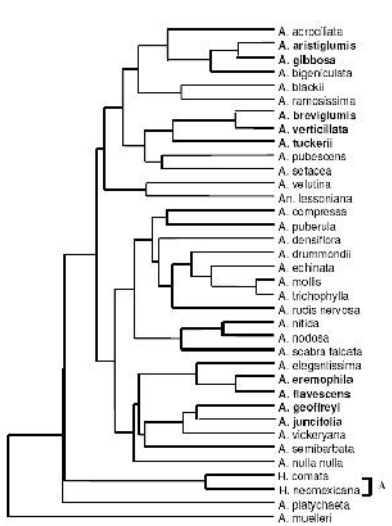


**Figure 3**

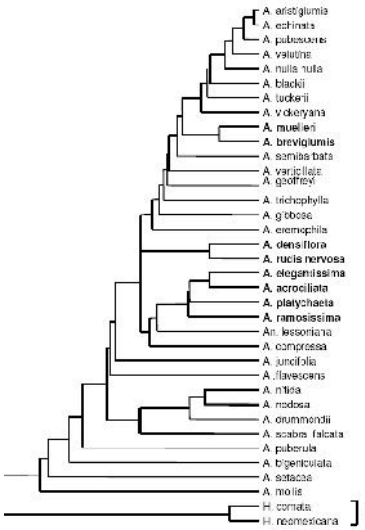


**Figure 4**

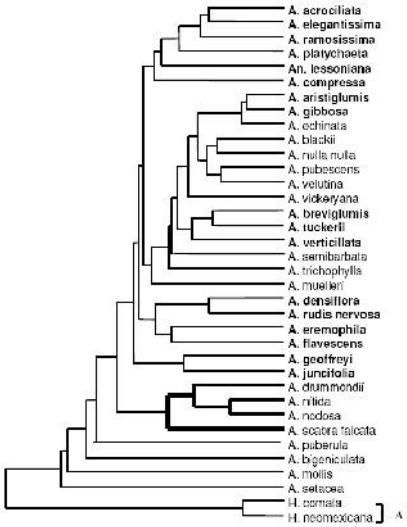


**Figure 5**

**Figure 1.** Parsimony analysis of mico morphological data. A is the outgroup. Strict consensus of 25,698 equally parsimonious tress (140 steps, CI = 0.32, RI = 0.57, RC = 0.19). Bootstrap percentage values (1000 replicates) are shown above the branches for all values > 50.

**Figure 2.** Parsimony analysis of the molecular data. A is the outgroup. Strict consensus of 2, 808 equally parsimonious tress (292 steps, CI = 0.49, RI = 0.61, RC = 0.3). Thicker lines indicate the group was also identified in the UPGMA analyses. Groups in bold case indicate the groups identified in the UPGMA analysis of the molecular data. Bootstrap percentage values (1000 replicates) are shown above the branches for all values > 50.

**Figure 3.** UPGMA analysis of the micro morphological data. Thicker lines indicate the group also was identified in parsimony analysis of the molecular data and other UPGMA analyses. Groups in bold case indicate the groups also identified in the UPGMA analysis of combined data.

**Figure 4.** UPGMA analysis of the molecular data. Thicker lines indicate the group also was identified in other analyses. Bold case indicates the groups identified in the parsimony analysis of the molecular data.

**Figure 5.** UPGMA analysis of the combined data. Thicker lines indicate the group also was identified in parsimony analysis of the molecular data and other UPGMA analyses. Bold case indicates the groups identified in UPGMA analyses of both the micro morphological and molecular data.

is a little support for the subgeneric classification of *Austrostipa* proposed by Jacobs and Everett (1996) by the micro morphological analyses, the monophyly of *Austrostipa* received strong support (91%) from the parsimony analysis (Figure 1).

*Molecular analyses*

Unlike micro morphological analyses, most groups retrieved in the parsimony analysis of molecular data were also retrieved in the UPGMA analysis. Except for the outgroups, there are five groups that are resolved in the parsimony analysis and four groups in the UPGMA analysis (Figure 2 and Figure 4.). Moreover, most groups retrieved in the parsimony analysis of molecular data have quite strong bootstrap support (>70%).

The first group retrieved in the parsimony analysis consists of four species: *A. drummondii*, *A. nitida*, *A. nodosa* and *A. scabra* subsp. *falcata*. All four species in the group are placed in the subgenus *Falcatae* by Jacobs and Everett (1996). This group received 92% bootstrap support and also is supported by UPGMA analyses of the micro morphological and molecular data (Figure 2, Figure 3 and Figure 4). In the UPGMA analysis of the molecular data, the group contains four species, while in the UPGMA analysis of the micro morphological and molecular data the group contains three species, without *A. drummondii* (Figure 3 and Figure 4). In addition, in the UPGMA analysis of the molecular data, *A. nitida* placed together with *A. nodosa*, as in the UPGMA analysis of the micro morphological data, while in the parsimony analysis, *A. nitida* placed with *A. drummondii* and this clade receives weak bootstrap support (53%).

Morphologically, all *Falcatae* species are caespitose (growing in tufts), have culms that only branch in the inflorescence and, in addition, all have a falcate bristle on the awn, and hairy lemmas (Jacobs and Everett 1996). The spikelets are all so similar that vegetative characters often play an important role in distinguishing taxa in the *Falcatae*. It is often very difficult to tell *A. nitida* and *A. nodosa* apart. In spite the similarity, there are some differences among species. *Austrostipa scabra* is characterized by having very fine narrow leaves, much finer than the others in the subgenus. *A. drummondii* has hairy awns and leaves. *A. nitida* and *A. nodosa* are very similar, differing only in minor characteristics of the inflorescence but also in the basal formation of new culms, *A. nitida* being intravaginal and *A. nodosa* being extravaginal. The species also tend to grow in different habitats. *A. nitida* grows particularly on (mostly red) sandy soils in all mainland States, while *A. nodosa* grows on heavier soils than *A. nitida* in all regions in Australia except the North Coast and South Coast of New South Wales, Victoria, South Australia and Western Australia, often associated with mallee. *Austrostipa scabra* subsp. *falcata* grows mainly in the woodlands on the Tablelands and southern areas of New South Wales, Queensland, Victoria and South Australia (Vickery et al. 1986).

The second group that is resolved in the parsimony analysis of molecular data is the group that contains four species: *A. elegantissima*, *A. acrociliata*, *A. platychaeta* and *A. ramosissima*. This group was also resolved in the UPGMA analysis of molecular data and received 80% bootstrap support (Figure 2 and Figure 4). Although, *A. acrociliata* and *A. platychaeta* have been placed in the same subgenus (subgenus *Arbuscula*, Jacobs and Everett 1996), the analyses do not put those two as sister species. The analysis supported the grouping of *A. acrociliata* with *A. elegantissima* (Figure 2) but only with low bootstrap support (67%).

Morphologically, there are many similarities between *A. acrociliata* and *A. platychaeta*. For example, both species have linear-cylindrical to ovate-cylindrical panicles and glabrous, scabrous or pubescent branches and pedicels. Moreover, both species have branched culms, a blunt callus and the lemma longer than palea. They also share an almost-falcate awn. There has been some speculation as to their relationships with the well-defined *Falcatae* (S. Jacobs pers. comm.), though there is no other link and none of the analyses has supported any such connection. It is understandable that these species have been placed in the same subgenus but perhaps the characteristic growth form, which may relate to habitat and appears to be a homoplasious character, disguises significant differences.

In the recent classification of *Austrostipa* (Jacobs and Everett 1996), *A. elegantissima* is placed in subgenus *Petaurista* along with *A. tuckeri*. *A. elegantissima* is more similar to *A. tuckeri* than to *A. acrociliata* in terms of morphology. For example, both *A. elegantissima* and *A. tuckeri* have pyramidal panicles when mature and spreading, with whorled branches, and the whole unit detaches and acts as the diaspore, while *A. acrociliata* has linear-cylindrical to ovate- cylindrical panicles that remain attached and the florets break off separately. Moreover, both *A. elegantissima* and *A. tuckeri* have characteristic fine hairs on the branches and pedicels, while *A. acrociliata* has glabrous, scabrous or pubescent branches and pedicels. These hairs and the whole inflorescence detaching are characteristic of subgenus *Petaurista* (Jacobs and Everett 1996). *A. acrociliata* has glabrous, scabrous or pubescent branches and pedicels, which is the usual situation in *Austrostipa*. Despite the similarity between *A. elegantissima* and *A. tuckeri*, there are some differences. For example, hairs on the branches of *A. elegantissima* are longer than in *A. tuckeri*. *A. elegantissima* has hairs up to 2 mm long whereas *A. tuckeri* hairs up to only 0.5 mm long. *A. elegantissima* has glabrous nodes while *A. tuckeri* has nodes with sericeous hairs 0.6 mm long. While the inflorescence characters seem quite highly derived and suggest close relationship, any analyses that concentrate on other characteristics seem to consistently suggest that they are not particularly closely related (Jacobs et al. 2000). Wind dispersal does seem to have been derived several times in the Stipoid grasses (Jacobs and Everett 1997; Jacobs et al. 2000), and several obviously different syndromes have evolved. In every other case so far, species with the same syndrome have been shown to form a closely related group (Jacobs et al. 2000). Of all these syndromes, that developed in subgenus *Petaurista* is the most divergent (the whole inflorescence acting as a diaspore and the characteristic long-hairy branches and/or pedicels) and is the most difficult to imagine as being an example of

parallel evolution. The relationships here are still not clear and can probably only be solved by exploring other even more variables sites for genes sequences.

The third group that was recognized in both parsimony and UPGMA analysis of molecular data and received 81% bootstrap support is the group that consists of two species: *A. densiflora* and *A. rudis* subsp. *nervosa.* These species s are placed in two subgenera in the recent classification (Jacobs and Everett 1996). *A. densiflora* is in subgenus *Austrostipa* while *A. rudis* subsp. *nervosa* is in subgenus *Tuberculatae*. There are a lot of differences between the two species in term of gross morphology and habitat. For example, *A. densiflora* has a lemma that is hairy/scabrous near the apex and a characteristic long-hairy awn (one of the characteristics of subgenus *Austrostipa* (Jacobs and Everett 1996)), while *A. rudis* subsp. *nervosa* has a lemma that is glabrous for varying lengths below the lemma apex and which is covered with characteristic silicious crystalline blunt tubercles (characteristics of subgenus *Tuberculatae* (Jacobs and Everett 1996)). Both species also differ in their habitats. *A. densiflora* grows in low fertility soils and is more common after disturbance, in drier regions away from the coast of New South Wales, Queensland, Victoria and South Australia. *A. rudis* subsp. *nervosa* grows on sandstone, mostly in undisturbed, higher-rainfall coastal areas of New South Wales, Queensland and Victoria (Vickery et al. 1986).

Another group recognized in the parsimony analysis of molecular data (with 75% bootstrap support) is a group consisting two species: *A. mollis* and *A. tuckeri*. However, this group is not supported by the UPGMA analysis. Like most groups retrieved in the parsimony analysis of molecular data, the species in this group are placed in different subgenera in the recent classification (Jacobs and Everett 1996). *A. mollis* is in subgenus *Austrostipa* while *A. tuckeri* is in subgenus *Petaurista.*

The last group retrieved in the parsimony analysis of molecular data (with 71% bootstrap support) consists of two species: *A. muelleri* and *A. breviglumis*, supported by UPGMA analysis of molecular data (Figure 2 and Figure 4). This group again comprises two species that have been placed in different subgenera by Jacobs and Everett (1996). *A. muelleri* was placed in subgenus *Tuberculatae* while *A. breviglumis* was in subgenus *Arbuscula*. There are several differences between the two species in term of gross morphology. For instance, *A. breviglumis* has sturdy simply-branched culms, while *A. muelleri* has spreading, scrambling or decumbent much-branched culms. The parsimony analysis of molecular data also supports the monophyly of *Austrostipa* with 100% bootstrap support (Figure 2).

This research has not supported the subgenera of *Austrostipa* (Jacobs and Everett 1996) with the exception of subgenus *Falcatae*. While there are occasional hints of further relationships, there is nothing substantial. It is possible that the subgenera (Jacobs and Everett 1996) do not adequately reflect relationships within the genus, but then the analyses do not produce strong evidence for improving that classification.

As shown in the Consistency Index (Table 1), most micro morphological characters are considered to be highly homoplasious, the exception being stomata size (µm) and stomata subsidiary cell size (µm) abaxial surface, which made it difficult to get meaningful result at this level of relationships.

There are 26 micro morphological characters in the Table 1 whereas the complete data were collected for 28 characters. The two uninformative but variable characters with CI = 1 are: (i) Leaf adaxial surface different over and between veins. This character consists of two states, absent and present. With the exception of *A. muelleri*, all remaining species that were examined scored as 'present', (ii) Leaf adaxial stomata abundance. This character consist of three states, no stomata present, few stomata and abundant. As for the previous character, *A. muelleri* has only few stomata, while the reminder of species that were examined have abundant stomata.

**Table 1.** The consistency index (CI) value of all micro-morphological characters used can be seen in the table below. ad = adaxial, ab = abaxial

| No | Characters | CI |
|---|---|---|
| 1. | Leaf ad. silica bodies | 0.125 |
| 2. | Leaf ad. long cell wall morphology | 0.500 |
| 3. | Leaf ad. stomata size (µm) | 0.316 |
| 4. | Leaf ad. stomata subsidiary cell size (µm) | 0.308 |
| 5. | Leaf ad. stomata shape | 0.333 |
| 6. | Leaf ad. macrohairs presence | 0.125 |
| 7. | Leaf ad. macrohairs position | 0.500 |
| 8. | Leaf ad. prickles presence | 0.333 |
| 9. | Leaf ad. prickles position | 0.500 |
| 10. | Leaf ab. different over and between veins | 0.143 |
| 11. | Leaf ab. silica bodies presence | 0.333 |
| 12. | Leaf ab. silica bodies shape | 0.465 |
| 13. | Leaf ab. Long cell wall morphology | 0.333 |
| 14. | Leaf ab. Stomata abundance | 0.500 |
| 15. | Leaf ab. stomata size (µm) | 0.833 |
| 16. | Leaf ab. stomata subsidiary cell size (µm) | 0.800 |
| 17. | Leaf ab. macrohairs presence | 0.333 |
| 18. | Leaf ab. macrohairs position | 0.316 |
| 19. | Leaf ab. prickles presence | 0.167 |
| 20. | Leaf ab. prickles position | 0.125 |
| 21. | Lemma fundamental cell lenght | 0.300 |
| 22. | Lemma sidewall shape | 0.333 |
| 23. | Lemma sidewall thickness | 0.250 |
| 24. | Lemma endwall shape | 0.250 |
| 25. | Lemma short cell hooks | 0.167 |
| 26. | Lemma silica bodies presence | 0.333 |

Although in all analyses, *Anemanthele lessoniana* is consistently included within a monophyletic of *Austrostipa*, admittedly at several different positions, there is no suggestion that the genera be combined. There are some obvious gross morphological characters that can be used to distinguish *Anemanthele* from *Austrostipa*, including stamen number, hilum shape and lemma nerves and length (Jacobs and Everett 1996).

## CONCLUSION

Parsimony analysis highly supported the monophyly of *Austrostipa* (>90%). However, there is a little support for the generic classification of *Austrostipa* proposed by Jacobs and Everett (1996). Only the subgenus *Falcatae* is supported by all analyses. The micro morphological characters used are uninformative (too homoplasious), consider the consistency index value less than 1.

## ACKNOWLEDGMENTS

I would like to thank Surrey Jacobs, Joy Everett and Paul Adam as my supervisors. I also would like to thank all staff at Royal Botanic Gardens Sydney and all member of International Stipeae Working Group.

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