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Caryopsis micromorphological survey of the genus *Themeda* (Poaceae) and allied spathaceous genera in the Andropogoneae

Yu ZHANG[1,2], Xiaoying HU[1], Yunxiao LIU[1], Qing LIU[1,*]

[1]Key Laboratory of Plant Resources Conservation and Sustainable Utilization, South China Botanical Garden, Chinese Academy of Sciences, Guangzhou, P.R. China

[2]Graduate University of Chinese Academy of Sciences, Beijing, P.R. China

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Abstract: A caryopsis micromorphological survey of 15 species of the genus *Themeda* Forssk. (Poaceae) and 4 species of allied spathaceous genera in tribe Andropogoneae allowed the recognition of 2 types of caryopses based on the ventral face and embryo shape for the first time. One kind of caryopsis had a concave ventral face with a grooved embryo, and the other kind of caryopsis had a flat ventral face with a keel-shaped embryo. Although the ventral face and embryo shapes had limited taxonomic value at the infrageneric level, the caryopsis shapes, embryo proportion, and sculpturing patterns were found to be valuable taxonomic characters at the interspecific level in *Themeda*. Consistent micromorphological characters of style base persistence and dorsiventral compression were observed for the first time in the caryopses of representative species of spathaceous genera in the Andropogoneae.

Key words: Micromorphology, spathaceous genera, taxonomy

1. Introduction

The genus *Themeda* Forssk. (Andropogoneae, Poaceae) comprises 27 drought-tolerant species exhibiting considerable ecological and morphological diversity in tropical and subtropical arid areas (Chen and Phillips, 2006; Zhang and Liu, 2012). Northern India and Southwest China (Figure 1) were inferred as the center of diversity for the genus with 20 species (Zhang and Liu, 2012). Two sections of *Themeda* were recognized based on the characters of raceme: section *Primothemedae* S.L.Chen & T.D.Zhuang with homogamous spikelet pairs arranged at different levels, and section *Themeda* with homogamous spikelet pairs arranged at the same level in the raceme base (Chen and Zhuang, 1989; Chen and Phillips, 2006).

The spathaceous genera were characterized by compound panicles, with spatheoles intervening at the base of racemes and paraclades (repeating branches; Liu et al., 2005a) in the tribe Andropogoneae (Figure 2) (Clayton and Renvoize, 1986). *Themeda* and allied spathaceous genera, the members of a specialized lineage in the tribe (Skendzic et al., 2007; Soreng et al., 2009; Teerawatananon et al., 2011), were predominantly distributed in extreme habitats of arid rocky mountain slopes (authors' field observations). The ecological function of spatheoles remained mysterious for years (Sendulsky et al., 1986; Clayton, 1990; Long, 1999). Caryopses are significant raceme components enclosed by spatheoles; thus, caryopsis micromorphology surveys might provide clues to unravel the mystery of the ecological function of spatheoles in Andropogoneae.

Caryopsis micromorphology, as a reliable approach for assessing phylogenetic relationship, had been definitely recognized in Poaceae (Bogdan, 1966; Barthlott, 1981; Wang et al., 1986; Liu et al., 2005b). For example, an examination revealed that 7 subfamilies corresponded to 7 caryopsis subtypes for Chinese grasses (Wang et al., 1986). In another example, the caryopsis ventral face and embryo shape were valuable characters for recognizing 3 suprageneric groups in the gramineous subfamily Chloridoideae (Liu et al., 2005b). However, almost nothing was known about the caryopsis micromorphology of *Themeda* and allied spathaceous genera in the Andropogoneae.

The present study aims to: 1) give detailed descriptions of caryopses in 15 *Themeda* species and 4 species of allied spathaceous genera in the tribe Andropogoneae; 2) discuss the taxonomic value of caryopsis micromorphological characters at the suprageneric and interspecific level; and 3) evaluate the evolutionary tendency of the caryopsis micromorphological character in *Themeda*.

* Correspondence: liuqing@scbg.ac.cn

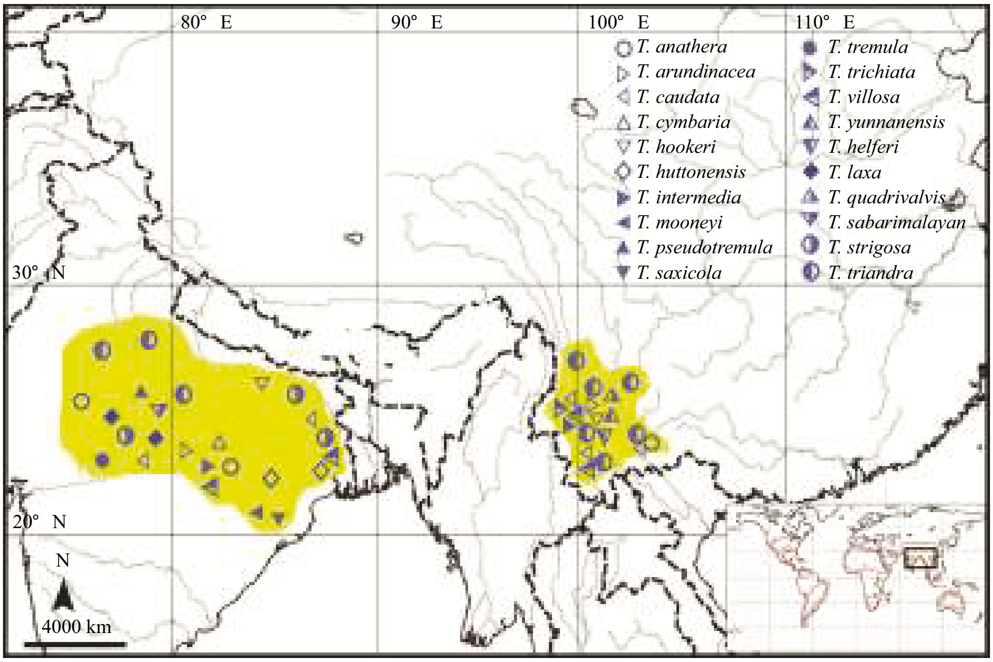

Figure 1. Distribution center of *Themeda* (yellow regions). Generic distribution regions shown by closed red lines in the lower right corner (color on the web only).

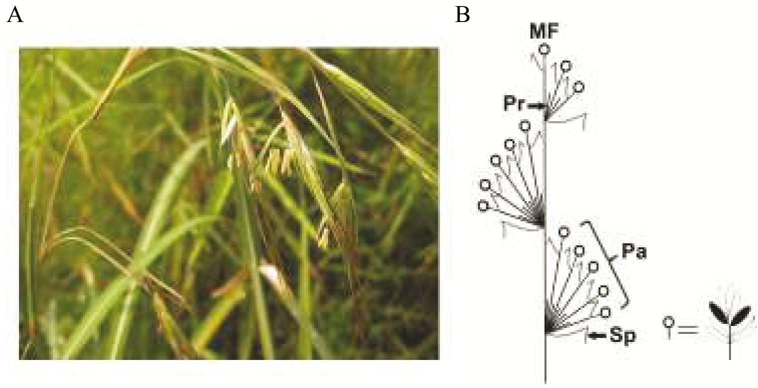

Figure 2. Spathaceous inflorescence (A) and diagram structure (B) of *Themeda caudata*. MF = main florescence, Pa = paraclade, Pr = prophyll, Sp = spatheole, hollow circle = raceme, hollow oblong = sterile spikelet, solid oblong = fertile spikelet (color on the web only).

2. Materials and methods

Mature caryopses of 15 species in *Themeda* and 4 species of allied spathaceous genera [5–16 caryopses for each species, excluding *T. unica* S.L.Chen & T.D.Zhuang and *Elymandra lithophila* (Trin.) Pilg.] were examined either from field collections or from herbarium specimens (Table 1). The length measurements of spatheole, lemma, and caryopsis were conducted under a Carl Zeiss Stemi SV 11 stereomicroscope (SM) (Carl Zeiss AG, Jena, Germany) and data are available upon request. Statistical analyses were conducted using Microsoft Excel 2007.

After shape observation and drawing with a Carl Zeiss SM, the caryopses were cleaned in a series of ethanol solutions (70%, 90%, and 100%) 3 times and then sputter-coated with gold in a JFC-1100 sputter coater (JEOL, Tokyo, Japan). Micromorphological characters were examined and photographed with a JEOL JSM-6360LV scanning electron microscope (SEM) at 10 kV. Caryopses were orientated with the stylopodium pointing up and the embryo pointing down. The dorsal face with embryo was orientated towards the lemma and the ventral face with sculptures was orientated towards the palea (Wang et al.,

Table 1. Material of *Themeda* [following the classifications of Chen and Phillips (2006) and The Plant List (2010)] and allied spathaceous genera examined in this study.

Species	Voucher	Location	No.	Figures
Themeda				
Section *Primothemedae* S.L.Chen & T.D.Zhuang				
T. anathera (Nees ex Steud.) Hack.	Walter K 22194 (US); PI 215612	India: Madhes	5	3A, 4B, 7A, 9A, 10A
T. arundinacea (Roxb.) A.Camus	Rock JF 825 (US) Mao PY 6793 (IBSC)	Burma: Chinwin District China : Yunnan	20	4D, 6B, 6C, 9B, 9C, 10C
T. avenacea (F.Muell.) Maiden & Betche	White CT 8736 (US)	Australia: Queensland	5	4E, 6D, 8I, 10D
T. caudata (Nees) A.Camus	Qing Liu 154 (IBSC)	China: Guangdong	5	3G, 7B, 9D, 10E
T. cymbaria Hack.	Clayton 5789 (US) V. Narayana Surasny s.n. (IBSC)	Ceylon: Nuwara Eliya District India	11	4F, 6E, 8J, 10F
T. gigantea (Cav.) Hack.	Anonymous 16764 (US) ; PI 247413 Ye HG 891 (IBSC)	Philippines: Luzon China: Guangdong	20	3B, 3H, 6F, 9E, 10G
T. hookeri (Griseb.) A.Camus	Qingzang Exped. 3168 (KIB)	China: Sichuan	6	3D, 7D, 8B, 10I
T. intermedia (Hack.) Bor	Waterhouse JH 952 (US)	New Guinea: Bismarck Archipelago	5	3I, 6G, 9F, 10J
T. unica S.L.Chen & T.D.Zhuang	Courtois P 12259 (NAS)	China: Anhui	1	7E, 8C, 11C
T. villosa (Poir.) A.Camus	Liborio EE 854 (US)	Philippines: Silangan Mt.	5	4G, 7F, 9J, 11D
T. yunnanensis S.L.Chen & T.D.Zhuang	Wu SK 362 (IBSC)	China: Yunnan	5	4H, 6J, 9I, 11E, 11F
Section *Themeda*				
T. arguens (L.) Hack.	Frank WG 13027 (US)	Ceylon: Peradeniya	5	4C, 6A, 8H, 10B
T. helferi Munro ex Hack.	Ban NL s.n. (US)	India: Madzae	5	3C, 7C, 8A, 10H
T. quadrivalvis (L.) Kuntze	Li YL et Ma WJ YDDXSB-158 (KIB)	China: Yunnan	8	3E, 6H, 9G, 11A
T. triandra Forssk.	Yang GH 69627 (KIB); ILCA 18381 Jiang B 1 (IBSC)	China: Sichuan China: Shandong	20	3J, 6I, 9H, 11B
Allied spathaceous genera				
Elymandra lithophila (Trin.) Clayton	Anonymous 11.763 (US)	Angola: Lunda	1	4I, 7G, 8D, 11G
Heteropogon contortus (L.) P.Beauv. ex Roem. & Schult.	Shauty HJ 227 (US) Zhang ZQ 10113 (IBSC)	Africa: Nyasaland China : Guangxi	20	4A, 7H, 8E, 11H
Hyparrhenia filipendula (Hochst.) Stapf	Anonymous 4022 (KIB) Davidse G 8915 (US)	China: Yunnan Sri Lanka, Uva	20	3F, 7I, 8F, 11I
Hyperthelia dissoluta (Nees ex Steud.) Clayton	Hitchcock AS 25002 (US)	Kenya: Eldoret	5	4J, 7J, 8G, 11J

Abbreviations: IBSC = Herbarium of South China Botanical Garden, Chinese Academy of Sciences (CAS); ILCA = International Livestock Centre for Africa, Addis Ababa, Ethiopia; KIB = Herbarium of Kunming Institute of Botany, CAS; NAS = Herbarium of Institute of Botany, Jiangsu Province and CAS; PI = Germplasm Resources Information Network of United States Department of Agriculture at Beltsville; US = United States National Herbarium.

1986; Terrell and Peterson, 1993). SEM photos were taken in the middle area of the ventral face for each sample. Terminology following Sendulsky et al. (1986), Stearn (1992), Terrell and Peterson (1993), Koul et al. (2000), and Bona (2013) was used.

3. Results

According to the corresponding relationship between ventral face and embryo morphology, 2 types of caryopses were observed in the examined taxa. A detailed description is given below.

Concave ventral face: Caryopses had concave ventral faces, convex dorsal faces, and grooved embryos. They were abbreviated as the CG type (Figure 3A).

Taxa with the CG type of caryopses: 5 species of section *Primothemedae* including *Themeda anathera*, *T. caudata*, *T. hookeri*, *T. unica*, and *T. villosa*; 1 species of section *Themeda*, namely *T. helferi*; and 4 species of allied spathaceous genera including *Elymandra lithophila*, *Hyparrhenia filipendula*, *Heteropogon contortus*, and *Hyperthelia dissoluta*.

Flat ventral face: Caryopses had relatively flat ventral faces, rounded dorsal faces, and keel-shaped embryos. They were abbreviated as the FK type (Figure 3B).

Taxa with the FK type of caryopses: 6 species of section *Primothemedae*, including *Themeda arundinacea*, *T. avenacea*, *T. cymbaria*, *T. gigantea*, *T. intermedia*, and *T. yunnanensis*, and 3 species of section *Themeda*, including *T. arguens*, *T. quadrivalvis*, and *T. triandra*.

In addition to the ventral face, 5 diagnostic characters, including caryopsis shape, caryopsis size, embryo shape, sculpturing patterns with different numbers of testa cells in 50 × 50 μm, and embryo proportion, were observed in *Themeda* and allied spathaceous genera (Table 2).

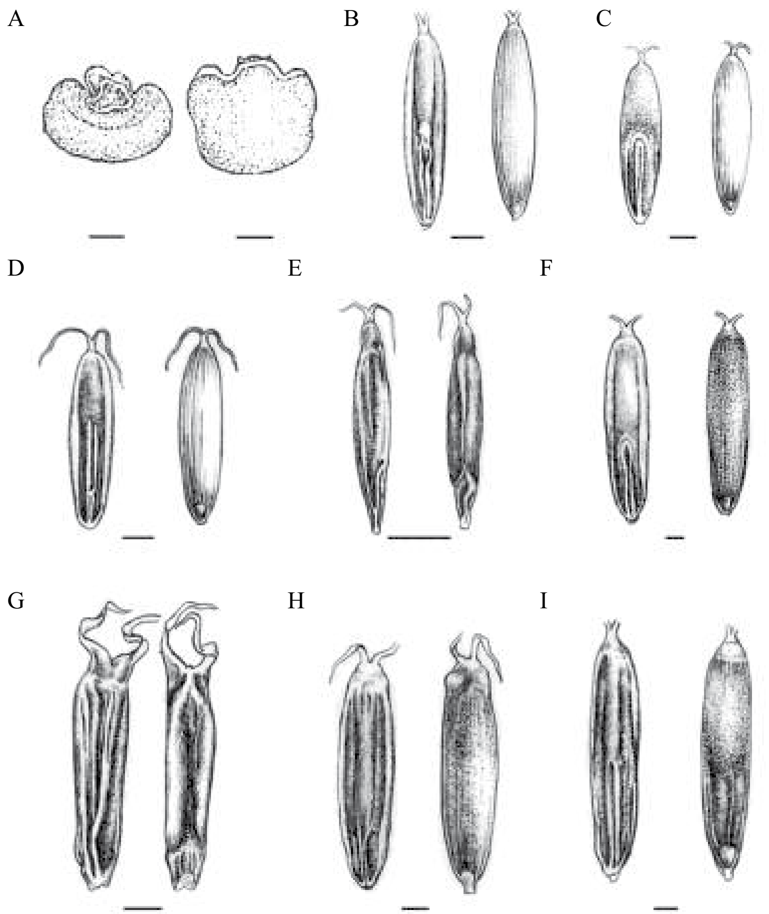

Figure 3. Caryopsis shapes of *Themeda* (SM). A- *T. anathera* with concave ventral face upward, B- *T. gigantea* with flat ventral face upward, C- *T. helferi*, D- *T. hookeri*, E- *T. quadrivalvis*, F- *Hyparrhenia filipendula*, G- *T. caudata*, H- *T. gigantea*, I- *T. intermedia*, J- *T. triandra*. Dorsal face and ventral face located on left side and right side, respectively. Scale bars = 0.5 mm.

Table 2. Caryopsis micromorphological characters of *Themeda* and allied spathaceous genera.

Taxa	VF	E	SH	SC	TN	LE (mm)	WI (mm)	TH (mm)	P
Sect. *Primothemedae*									
T. anathera	CC	G	LL	II	2–3	3.03–(3.16)–3.27	0.88–(0.95)–1.04	0.47–(0.67)–0.78	0.62–0.76
T. arundinacea	FL	K	LL	II	1–2	3.48–(4.34)–4.93	0.95–(1.05)–1.06	0.44–(0.79)–0.87	0.40–0.65
T. avenacea	FL	K	LL	II	3–9	3.42–(5.43)–7.38	0.98–(1.27)–1.46	0.76–(1.12)–1.40	0.41–0.71
T. caudata	CC	G	OB	II	4–5	4.39–(5.14)–5.58	1.08–(1.34)–1.52	0.76–(1.05)–1.26	0.48–0.51
T. cymbaria	FL	K	LL	II	7–9	1.90–(2.03)–2.15	0.62–(0.63)–0.64	0.28–(0.41)–0.50	0.60–0.63
T. gigantea	FL	K	OB	II	3–5	1.81–(3.33)–4.32	0.35–(0.89)–1.19	0.53–(0.86)–0.94	0.50–0.63
T. hookeri	CC	G	FF	I	4–5	3.20–(4.04)–4.49	0.95–(1.08)–1.21	0.72–(0.87)–1.03	0.50–0.63
T. intermedia	FL	K	OB	II	1–2	2.27–(3.08)–4.40	0.50–(0.79)–1.31	0.26–(0.52)–1.04	0.42–0.52
T. unica	CC	G	LL	I	1–2	5.28	2.42	1.63	0.74
T. villosa	CC	G	LL	II	2–3	3.78–(4.20)–4.71	1.08–(1.14)–1.23	0.86–(0.91)–1.00	0.46–0.51
T. yunnanensis	FL	K	LL	II	2–3	4.53–(5.02)–5.50	1.30–(1.35)–1.41	0.98–(1.02)–1.07	0.51–0.63
Sect. *Themeda*									
T. arguens	FL	K	LL	II	2–4	2.89–(3.035)–3.18	0.57–(0.665)–0.76	0.48–(0.545)–0.61	0.39–0.44
T. helferi	CC	G	FF	I	3–4	2.52–(2.90)–3.37	0.58–(0.78)–0.89	0.47–(0.59)–0.73	0.49–0.53
T. quadrivalvis	FL	K	FF	II	3–7	3.18–(3.84)–4.53	0.81–(1.00)–1.29	0.66–(0.86)–1.19	0.51–0.58
T. triandra	FL	K	OB	II	3–5	3.68–(4.74)–5.71	0.70–(1.19)–1.35	0.68–(0.99)–1.06	0.48–0.63
Allied spathaceous genera									
Elymandra lithophila	CC	G	LL	I	3–5	4.56	1.04	0.89	0.42
Heteropogon contortus	CC	G	OB	I	3–4	3.58–(4.07)–4.78	0.59–(0.63)–0.74	0.37–(0.51)–0.61	0.50–0.65
Hyparrhenia filipendula	CC	G	FF	I	2–4	2.09–(2.10)–2.12	0.40–(0.65)–0.72	0.35–(0.42)–0.44	0.34–0.35
Hyperthelia dissoluta	CC	G	LL	I	3–5	2.81–(3.70)–4.59	0.79–(1.015)–1.24	0.56–(0.755)–0.95	0.47–0.55

Abbreviations: VF = ventral face [CC = concave; FL = flat]; E = embryo [G = grooved; K = keel-shaped]; SH = shape [OB = oblong; LL = lanceolate; FF = fusiform]; SC = sculpturing pattern [I = undulating reticulate pattern; II = straight reticulate pattern]; TN = number of testa cells in 50 × 50 µm; LE = minimum–(mean)–maximum values of length of caryopses (mm); WI = minimum–(mean)–maximum values of width of caryopses (mm); TH = minimum–(mean)–maximum values of thickness of caryopses (mm); P = embryo proportion.

Caryopsis shape was described by the view of the surface outline (Clayton et al., 2002 onwards) and 3 types of caryopsis shapes were observed in the examined taxa:

(I) Fusiform caryopses were the widest in the middle part, tapering off to both ends. Fusiform caryopses were observed in *Themeda helferi* (Figure 3C), *T. hookeri* (Figure 3D), *T. quadrivalvis* (Figure 3E), and *Hyparrhenia filipendula* (Figure 3F).

(II) Oblong caryopses were almost the same length along each side. This kind of caryopsis was observed in *Themeda caudata* (Figure 3G), *T. gigantea* (Figure 3H), *T. intermedia* (Figure 3I), *T. triandra* (Figure 3J), and *Heteropogon contortus* (Figure 4A).

(III) The lanceolate caryopsis length was at least 3 times that of the width, and the length side tapered off to the embryo end. This kind of caryopsis shape was observed in *Themeda anathera* (Figure 4B), *T. arguens* (Figure 4C), *T. arundinacea* (Figure 4D), *T. avenacea* (Figure 4E), *T. cymbaria* (Figure 4F), *T. unica* (similar to *T. villosa*), *T. villosa* (Figure 4G), *T. yunnanensis* (Figure 4H), *Elymandra lithophila* (Figure 4I), and *Hyperthelia dissoluta* (Figure 4J).

Caryopsis mean size varies greatly in the examined taxa, from 2.03 mm length × 0.63 mm width × 0.41 mm thickness in *Themeda cymbaria* to 5.28 mm length × 2.42 mm width × 1.63 mm thickness in *T. unica* (Table 2). In general, there was a positive correlation between the caryopsis length and lemma length ($R^2 = 0.3959$, $P = 0.01$; Figure 5A), i.e. longer lemmas tended to surround longer caryopses. The correlation between caryopsis and lemma length was also found in several gramineous subfamilies, which might reflect reproductive adaptability rather than a phylogenetic relationship in Poaceae (Wang et al., 1986; Liu et al., 2005b). We also observed a positive correlation between the length of a caryopsis and its surrounding spatheole ($R^2 = 0.3650$, $P = 0.01$; Figure 5B). In other words,

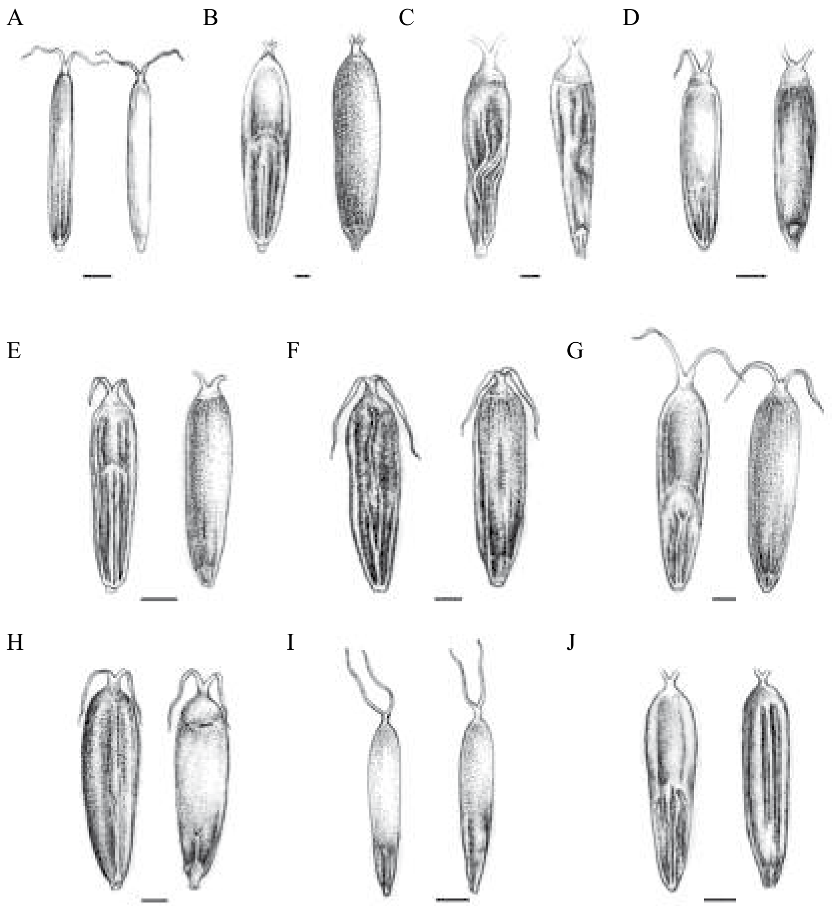

Figure 4. Caryopsis shapes of *Themeda* and allied spathaceous genera (SM). A- *Heteropogon contortus*, B- *T. anathera*, C- *T. arguens*, D- *T. arundinacea*, E- *T. avenacea*, F- *T. cymbaria*, G- *T. villosa*, H- *T. yunnanensis*, I- *Elymandra lithophila*, J- *Hyperthelia dissoluta*. Dorsal face and ventral face located on left side and right side, respectively. Scale bars = 0.5 mm.

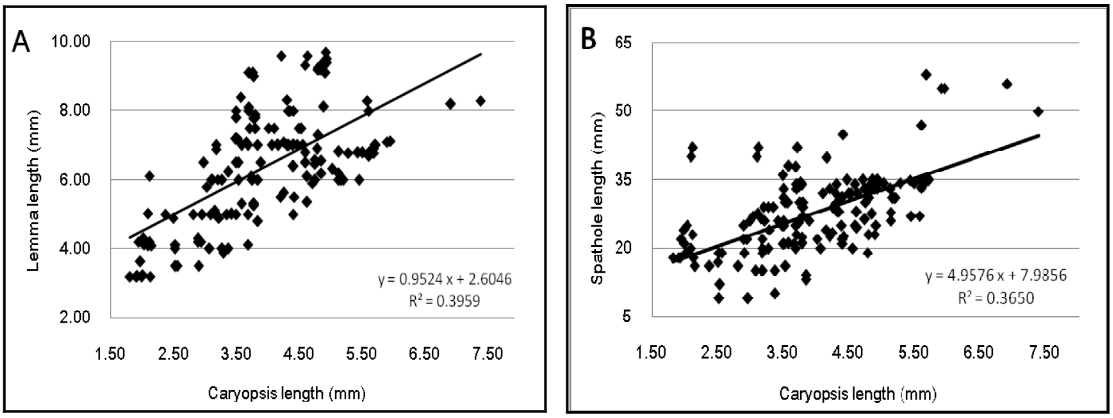

Figure 5. A- Correlation analyses between the caryopsis and lemma length and B- between the caryopsis and spatheole.

longer caryopses were packaged by longer spatheoles, and likewise it was easy to understand that the longer spatheoles embraced the longer raceme components, including caryopses. Two kinds of embryo shapes in the examined taxa were observed:

(I) Keel-shaped in *Themeda arguens* (Figure 6A), *T. arundinacea* (Figures 6B and 6C), *T. avenacea* (Figure 6D), *T. cymbaria* (Figure 6E), *T. gigantea* (Figure 6F), *T. intermedia* (Figure 6G), *T. quadrivalvis* (Figure 6H), *T. triandra* (Figure 6I), and *T. yunnanensis* (Figure 6J).

(II) Grooved in *Themeda anathera* (Figure 7A), *T. caudata* (Figure 7B), *T. helferi* (Figure 7C), *T. hookeri* (Figure 7D), *T. unica* (Figure 7E), *T. villosa* (Figure 7F), *Elymandra lithophila* (Figure 7G), *Heteropogon contortus* (Figure 7H), *Hyparrhenia filipendula* (Figure 7I), and *Hyperthelia dissoluta* (Figure 7J).

Two sculpturing patterns in the examined taxa were observed:

(I) Undulating reticulate pattern: undulate cell walls in *Themeda helferi* (Figure 8A), *T. hookeri* (Figure 8B), *T. unica* (Figure 8C), *Elymandra lithophila* (Figure 8D), *Heteropogon contortus* (Figure 8E), *Hyparrhenia filipendula* (Figure 8F), and *Hyperthelia dissoluta* (Figure 8G). The number of testa cells in 50 × 50 µm varied from 1–2 in *T. unica* to 4–5 in *T. hookeri*.

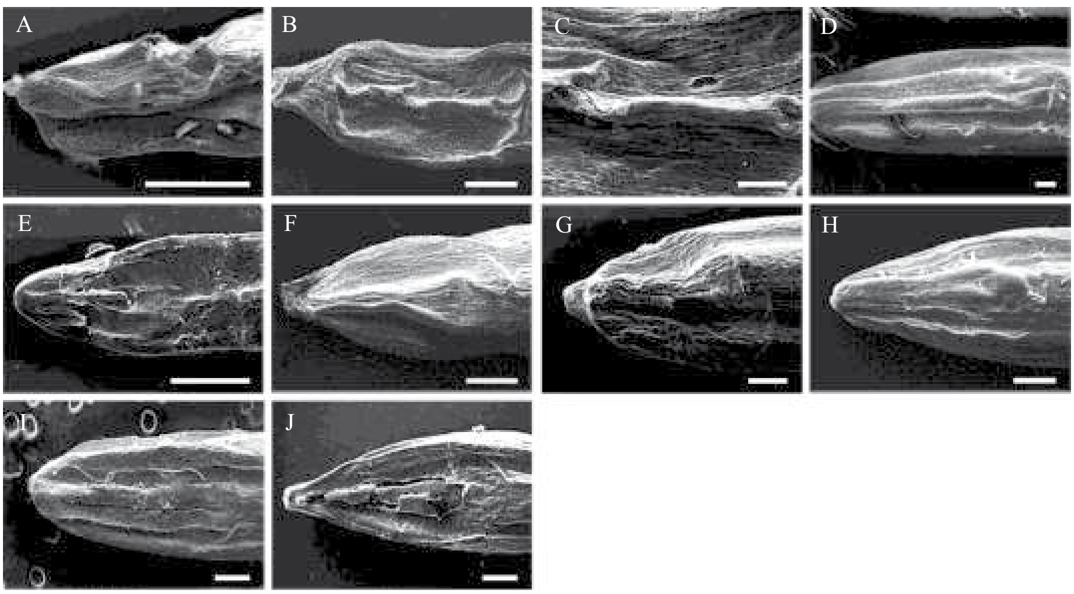

Figure 6. Embryo shapes of *Themeda* and allied spathaceous genera (SEM). A- *T. arguens*, B- *T. arundinacea*, C- detail of *T. arundinacea*, D- *T. avenacea*, E- *T. cymbaria*, F- *T. gigantea*, G- *T. intermedia*, H- *T. quadrivalvis*, I- *T. triandra*, J- *T. yunnanensis*. Scale bars = 500 µm.

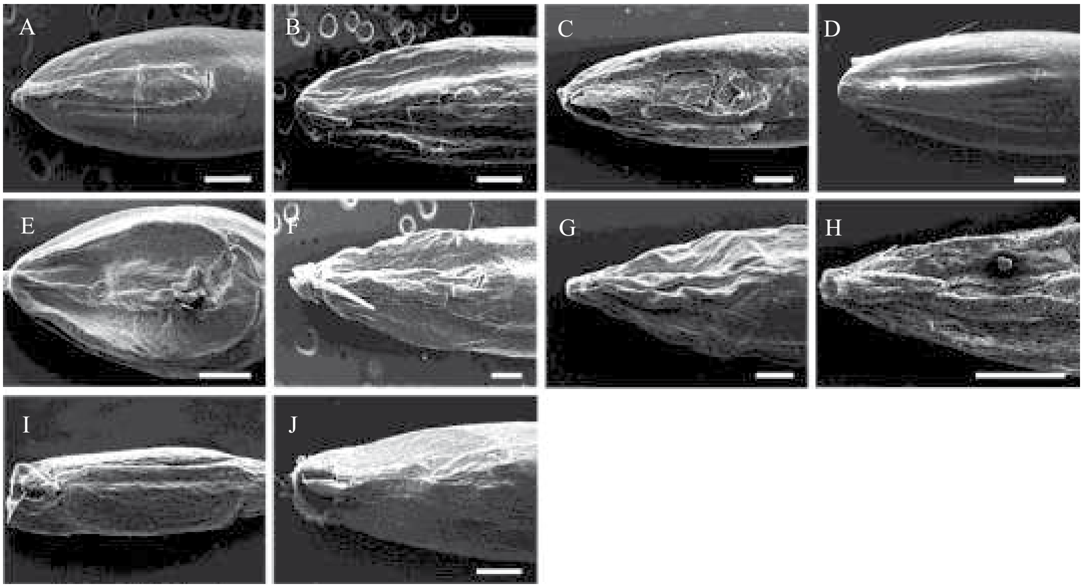

Figure 7. Embryo shapes of *Themeda* and allied spathaceous genera (SEM). A- *T. anathera*, B- *T. caudata*, C- *T. helferi*, D- *T. hookeri*, E- *T. unica*, F- *T. villosa*, G- *Elymandra lithophila*, H- *Heteropogon contortus*, I- *Hyparrhenia filipendula*, J- *Hyperthelia dissoluta*. Scale bars = 500 µm.

(II) Straight reticulate pattern: straight cell walls in *Themeda arguens* (Figure 8H), *T. avenacea* (Figure 8I), *T. cymbaria* (Figure 8J), *T. anathera* (Figure 9A), *T. arundinacea* (Figures 9B and 9C), *T. caudata* (Figure 9D), *T. gigantea* (Figure 9E), *T. intermedia* (Figure 9F), *T. quadrivalvis* (Figure 9G), *T. triandra* (Figure 9H), *T. yunnanensis* (Figure 9I), and *T. villosa* (Figure 9J). The straight cell walls of *T. cymbaria* are extremely irregular (Figure 8J). The number of testa cells in 50 × 50 µm varied from 1–2 in *T. arundinacea* to 7–9 in *T. cymbaria*.

Embryo proportion of the examined taxa varied from 0.34–0.35 in *Hyparrhenia filipendula* to 0.62–0.76 in *Themeda anathera*.

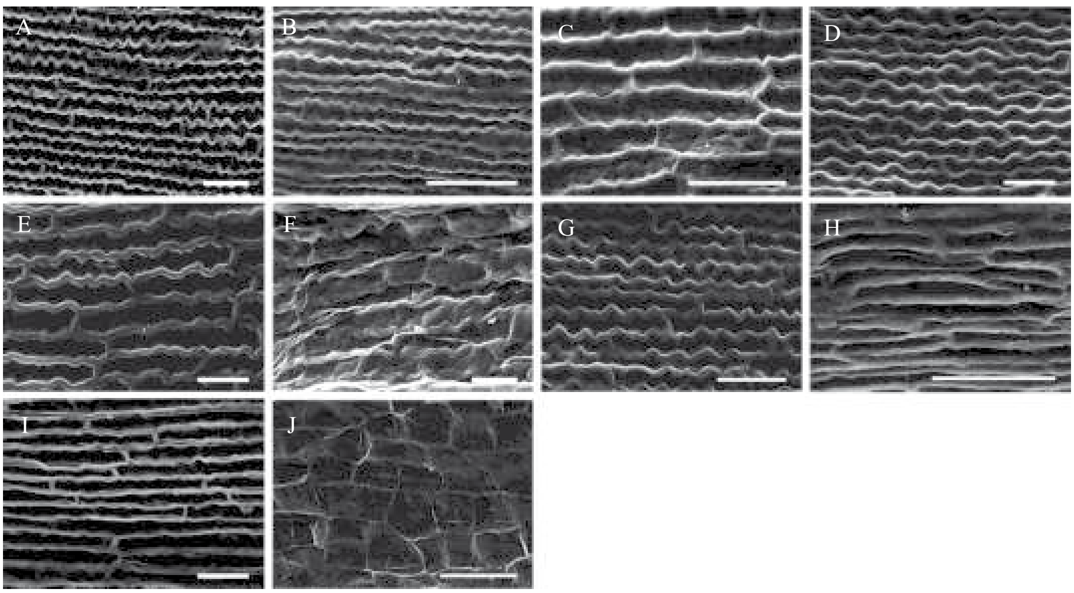

Figure 8. Caryopsis sculpture pattern of *Themeda* and allied spathaceous genera (SEM). A–G: Undulating reticulate pattern. A- *T. helferi*, B- *T. hookeri*, C- *T. unica*, D- *Elymandra lithophila*, E- *Heteropogon contortus*, F- *Hyparrhenia filipendula*, G- *Hyperthelia dissoluta*. H–I- Straight reticulate pattern. H- *T. arguens*, I- *T. avenacea*, J- *T. cymbaria*. Scale bars = 50 µm.

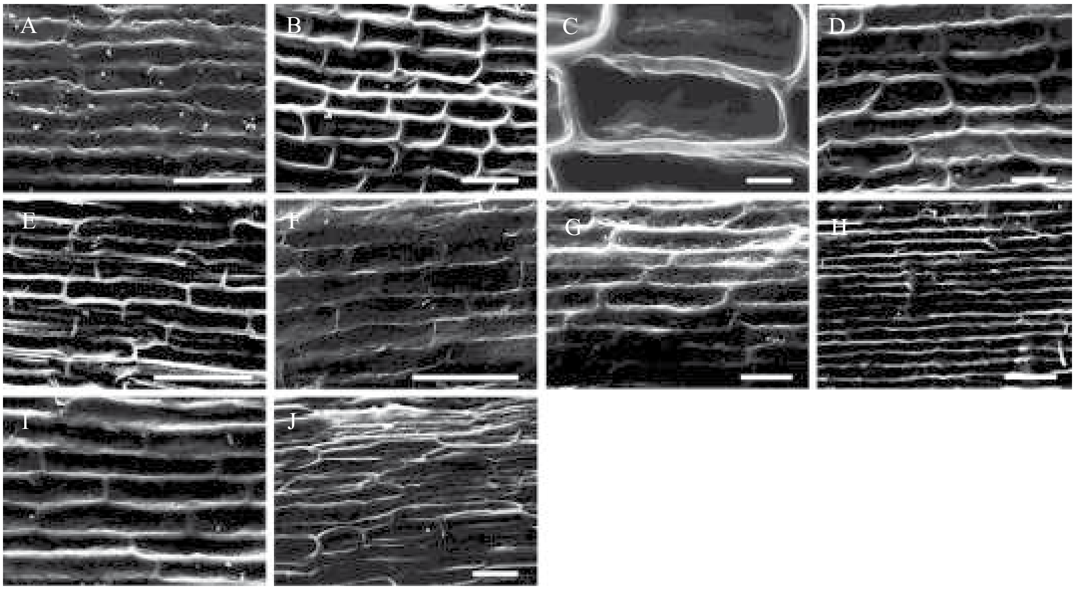

Figure 9. Caryopsis sculpturing patterns of straight reticulate patterns of *Themeda* and allied spathaceous genera (SEM). A- *T. anathera*, B- *T. arundinacea*, C- detail of *T. arundinacea*, D- *T. caudata*, E- *T. gigantea*, F- *T. intermedia*, G- *T. quadrivalvis*, H- *T. triandra*, I- *T. yunnanensis*, J- *T. villosa*. Scale bars = 50 µm.

Style base persistence for all examined taxa: *Themeda anathera* (Figure 10A), *T. arguens* (Figure 10B), *T. arundinacea* (Figure 10C), *T. avenacea* (Figure 10D), *T. caudata* (Figure 10E), *T. cymbaria* (Figure 10F), *T. gigantea* (Figure 10G), *T. helferi* (Figure 10H), *T. hookeri* (Figure 10I), *T. intermedia* (Figure 10J), *T. quadrivalvis* (Figure 11A), *T. triandra* (Figure 11B), *T. unica* (Figure 11C), *T. villosa* (Figure 11D), *T. yunnanensis* (Figures 11E and 11F), *Elymandra lithophila* (Figure 11G), *Heteropogon contortus* (Figure 11H), *Hyparrhenia filipendula* (Figure 11I), *Hyperthelia dissoluta* (Figure 11J). Caryopsis compression of all examined taxa was dorsiventral. Results are summarized in Table 2.

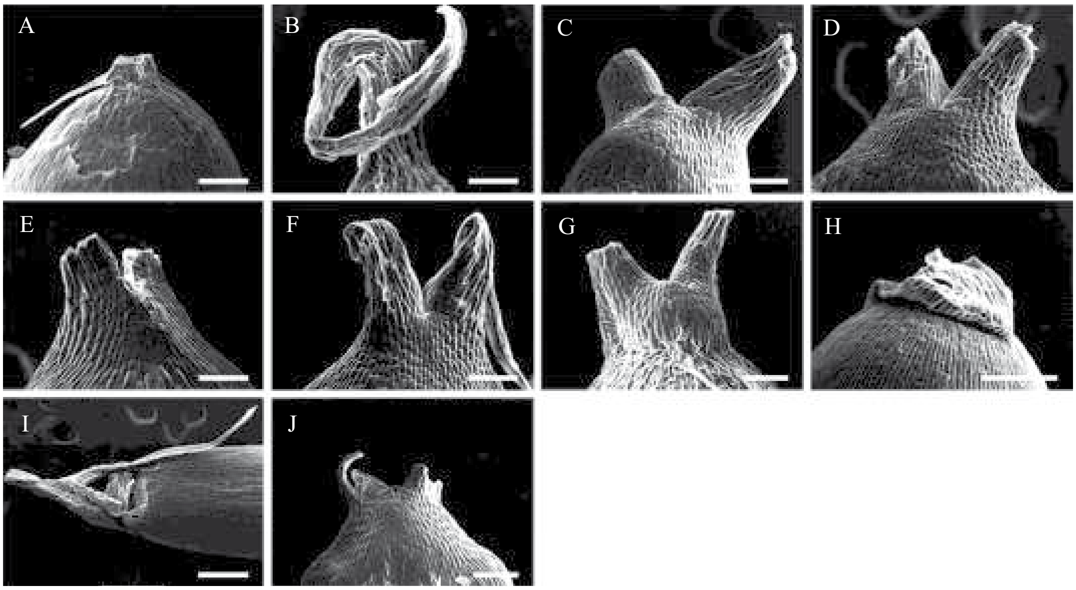

Figure 10. Stylopodia of *Themeda* and allied spathaceous genera (SEM). A- *T. anathera*, B- *T. arguens*, C- *T. arundinacea*, D- *T. avenacea*, E- *T. caudata*, F- *T. cymbaria*, G- *T. gigantea*, H- *T. helferi*, I- *T. hookeri*, J- *T. intermedia*. Scale bars = 200 µm.

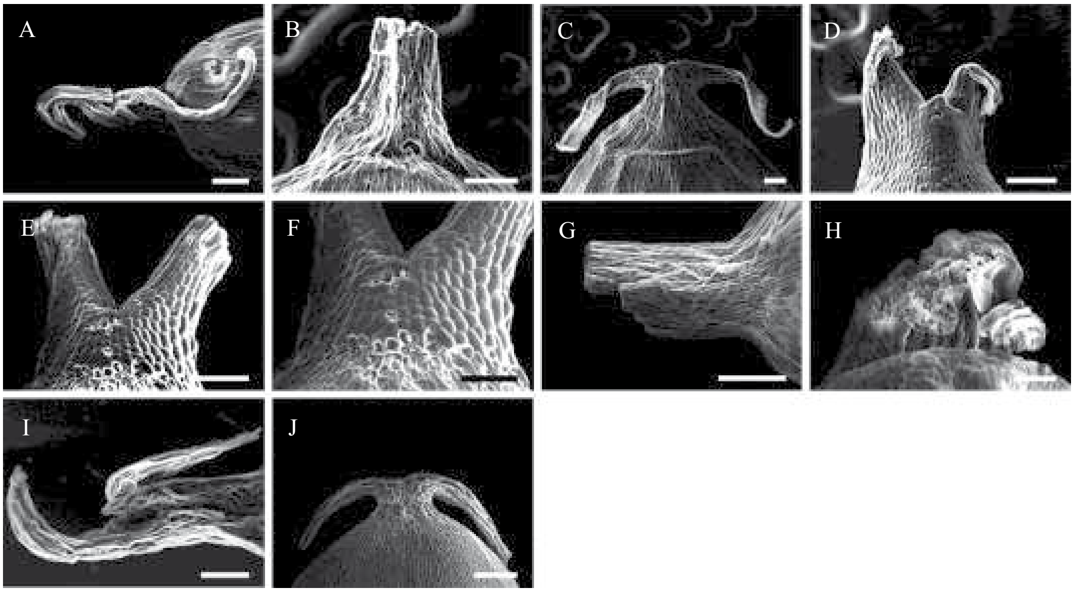

Figure 11. Stylopodia of *Themeda* and allied spathaceous genera (SEM). A- *T. quadrivalvis*, B- *T. triandra*, C- *T. unica*, D- *T. villosa*, E- *T. yunnanensis*, F- detail of *T. yunnanensis*, G- *Elymandra lithophila*, H- *Heteropogon contortus*, I- *Hyparrhenia filipendula*, J- *Hyperthelia dissoluta*. Scale bars = 200 µm.

4. Discussion

The caryopses of *Themeda* and allied spathaceous genera had the following principal diagnostic characters: 1) caryopses' mean size as 2.03–5.28 mm length × 0.63–2.42 mm width × 0.41–1.63 mm thickness in the examined taxa; 2) fusiform, oblong, or lanceolate caryopsis shapes; 3) concave or flat ventral faces; 4) grooved or keel-shaped embryos; 5) straight-reticulate or undulating-reticulate surface sculpturing patterns with 1–9 testa cells in 50 × 50 µm; 6) embryo proportions falling within the range of 0.34–0.76.

The ventral face and embryo shapes had limited taxonomic significance at the supraspecific level in *Themeda*. For example, the taxa in the same section had both the CG type and the FK type of caryopses. The CG type was shared by 6 species of section *Primothemedae* and 3 species of section *Themeda*, and the FK type was shared by 5 species of section *Primothemedae* and 1 species of section *Themeda* (Table 2). Neither type of caryopses was characterized by one section of *Themeda* specifically.

The caryopsis evolutionary tendency has been proposed to move from a concave face to a flat ventral face (Wang et al., 1986; Liu et al., 2005b). First, the relatively primitive subfamily Pooideae was characterized by concave ventral faces of caryopses, while the relatively advanced subfamily Panicoideae was characterized by flat ventral faces of caryopses in Poaceae (Wang et al., 1986; Sánchez-Ken et al., 2007; Bouchenak-Khelladi et al., 2008; Soreng et al., 2009; Sánchez-Ken and Clark, 2010). Second, while concave ventral faces had been observed in the young caryopses of *Themeda triandra*, their mature caryopses exhibited flat ventral faces. This phenomenon is defined as neoteny, or a plant's retention of ancestral features in its infancy stage (Stebbins, 1986). Third, 4 species in allied spathaceous genera had concave ventral faces in caryopses. Thus, our study indicated that the concave ventral face state was more primitive than the flat ventral face state in *Themeda*.

Spikelets and caryopses of *Themeda anathera* were conferred by some primitive characters states in the section *Primothemedae* (Zhang and Liu, 2012). Spikelet morphology of *T. anathera* was very distinct in the section *Primothemedae*, as homogamous spikelet pairs with rigid tubercle-based bristles on the margins and raceme with 1–3 spikelet pairs; however, the other species in the section *Primothemedae* were characterized by homogamous spikelet pairs with flexible tubercle-based hairs on the margins and raceme with fewer 1–2 spikelet pairs than *T. anathera* (Chen and Phillips, 2006). *Themeda anathera* was characterized by the CG type of caryopses and embryo proportions larger than 1/2 (0.62–0.76), which were hypothesized as relatively conservative and primitive character states of caryopses in Poaceae (Sendulsky et al., 1986; Wang et al., 1986). However, the robust conclusion for whether *T. anathera* was a relatively primitive member in the section *Primothemedae* or not might be supported not only by spikelet and caryopsis characters but also by future molecular phylogeny research.

Caryopsis shapes, embryo proportions, and sculpturing patterns were valuable diagnostic characters at the interspecific level in *Themeda*. The CG type of caryopses in *T. hookeri* and *T. caudata* had very similar characters, such as caryopsis size, embryo proportion, and compression (Table 2), while the distinct difference between the 2 species was caryopsis shape: fusiform caryopses presented in *T. hookeri* (Figure 3D) and oblong caryopses presented in *T. caudata* (Figure 3G). *Themeda unica* and *T. arguens*, sharing similar lanceolate caryopses, can be distinguished by embryo proportions: embryo proportion is less than 1/2 (0.39–0.44) in *T. arguens* and is more than 1/2 (0.74) in *T. unica* (Table 2). *Themeda villosa* and *T. helferi*, sharing CG types of caryopses and embryo proportions of nearly 1/2, can be identified by the straight reticulate sculpturing pattern in *T. villosa* (Figure 4G) and the undulating reticulate sculpturing pattern in *T. helferi* (Figure 3C).

Consistent micromorphological characters of style base persistence and dorsiventral compression were described for the first time in the caryopses of representative species of spathaceous genera in the tribe Andropogoneae. Certain caryopsis characters had been proposed to be the consequence of an adaptive process that increased the pollen collection efficiency of stigma. Style base persistence was associated with length and width of style branches (Figure 2A). During the transient flowering stage, 2 style branches stretched out from 2 sides between wide and flat lemmas and palea. Subsequently, style branches might be long and strong enough to keep style base persistence until the caryopsis is mature. In a compound panicle, the pollen collection efficiency of stigma could be improved by the extended space range covering the width between 2 style branches along the horizontal level and the length of 2 style branches along the vertical level, a pattern that was of particular value for spathaceous genera to adapt to the irregularities of the onset and end of rainy seasons in tropical arid areas (Stebbins, 1986; Friedman and Harder, 2005; Jiang et al., 2011). Therefore, it was not surprising to observe the caryopses of spathaceous genera having consistent characters of style base persistence and dorsiventral compression (Clayton, 1969).

In conclusion, caryopsis micromorphological characters had limited taxonomic value at the supraspecific level, while the caryopsis shape, embryo proportion, and sculpturing patterns (including number of testa cells in 50 × 50 µm) were valuable diagnostic characters at the interspecific level in *Themeda*. Consistent micromorphological characters of the style base persistence and dorsiventral compression were described for the first time for the caryopses of representative species of spathaceous genera in the tribe Andropogoneae.

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