A re-evaluation of the taxonomic status of the Australian species of *Arthraxon* Beauv. and *Thelepogon* Roth (Poaceae: *Panicoideae*: *Andropogoneae*)

E.J. Thompson

Summary

Thompson, E.J (2019). A re-evaluation of the taxonomic status of the Australian species of *Arthraxon* Beauv. and *Thelepogon* Roth (Poaceae: *Panicoideae*: *Andropogoneae*). ***Austrobaileya*** **10(3): 480–505.** The new combination *Arthraxon australiensis* (B.K.Simon) E.J.Thomps. is made based on *Thelepogon australiensis* B.K.Simon following detailed comparison of *A. castratus* (Griff.) Narayanaswami ex Bor and *T. elegans* Roth ex Roem. & Schult. using gross morphology, micromorphology and anatomy.

Key Words: Poaceae; *Panicoideae*; *Andropogoneae*; *Arthraxoninae*; *Arthraxon*; *Arthraxon australiensis*; *Arthraxon castratus*; *Thelepogon australiensis*, *Thelepogon elegans*; Australia flora; Queensland flora; anatomy; micromorphology; new combination

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Introduction

Arthraxon Beauv. and *Thelepogon* Roth comprise mostly tropical to subtropical grasses belonging to the tribe *Andropogoneae* Dumort. in the subfamily *Panicoideae* Link. The tribe is distinguished by paired spikelets, sessile and pedicellate (the latter sometimes reduced or absent), with the sessile ones bearing the upper lemma (fertile) typically with a geniculate awn comprising a spiralled column with a bristle (Bentham 1881; Clayton 1973; Clayton & Renvoize 1986; Watson & Dallwitz 1992; Kellogg 2015). However, the placement of *Arthraxon* and *Thelepogon* at subtribal level has vacillated. Bentham (1881) distinguished four subtribes and placed *Arthraxon* in *Arthraxeae* Benth. and *Thelepogon* in *Andropogoneae* Benth. (as *Euandropogoneae* Benth.). He defined *Arthraxeae* by the pedicellate spikelet absent and sometimes the pedicel lacking and *Andropogoneae* by the heterogamous spikelet-pair. Bentham (1881) remarked that the spikelets of *Thelepogon*, although having similarities to *Ischaemum* L. (*Andropogoneae*), are "remarkable for the rigid tuberculate …. glumes". Clayton (1972) used numerical analysis of morphological data to define seven subtribes and placed *Arthraxon* in subtribe *Arthraxoninae* Benth. and *Thelepogon* in subtribe *Ischaeminae* J.Presl. Clayton & Renvoize (1986) used a "pragmatic" morphological approach to distinguish eleven subtribes of which seven comprise the awned genera that mostly overlap with the classification by Clayton (1972) although *Arthraxon* was placed in subtribe *Andropogoninae* but *Thelepogon* remained in *Ischaeminae*. *Andropogoneae* and *Ischaeminae* were considered by Clayton & Renvoize (1986) to be closely related and often difficult to separate, primarily differing by the latter having a 2-keeled lower glume. Watson & Dallwitz (1992) recognised three subtribes and placed both genera in *Andropogoninae*. From molecular phylogenetic studies, Soreng *et al.* (2015) and Soreng *et al.* (2017) classified nine subtribes with *Arthraxon* in its own subtribe *Arthraxoninae* and *Thelepogon* in *incertae sedis*.

The various types of trichomes present on the leaves of species of *Andropogoneae* have been considered to be of taxonomic value in studies such as Khan *et al.* (2017), Nazir *et al.*

Accepted for publication 13 June 2019

(2013) and Ullah *et al.* (2011). The distinctive combination of ciliate margin and heart-shaped leaf base shared by *Arthraxon* and *Thelepogon* (**Figs. 1 & 2**), is very uncommon in *Andropogoneae* (Prain 1917; Hutchinson & Dalziel 1936; van Welzen 1981; Watson & Dallwitz 1992; Simon 1993; Davidse 1994). However, some species in other genera have one or the other of these characters, for example *Clausospicula* Lazarides has just ciliate margins (Lazarides *et al.* 1991). On the other hand, several genera in tribe *Paniceae* R.Br. have stem-clasping leaves but few, such as *Panicum* L., have this combination with ciliate margins (Watson & Dallwitz 1992). Simon (1993) considered that the difference in type of trichomes on the leaf margins to be one of the distinguishing characters between *Thelepogon elegans* Roth ex Roem. & Schult. and *T. australiensis* B.K.Simon.

Fig. 1. Cultivated plant of ***Arthraxon australiensis*** showing amplexicaule leaves with cilia on margins (*Thompson MOR803*, BRI). Image: E.J. Thompson.

Fig. 2. ***Thelepogon elegans*** from Hutchison & Dalziel (1936). Drawings show subdigitate inflorescences, caudate leaves and prop roots.

Prior to this paper, *Arthraxon* consisted of seven species and *Thelepogon*, two species. *Arthraxon* species are distributed across Africa, Asia, America and Australia (van Welzen 1981). Two species of *Arthraxon* have been recorded as indigenous for Australia, *viz*. *A*. *castratus* (Griff.) Narayanaswami ex Bor and *A*. *hispidus* (Thub.) Makino var. *hispidus* (Bostock & Holland 2017). The three records of *A*. *castratus* are from northern Queensland, although this species is otherwise known from India, Java, Sri Lanka and southern Vietnam. *A*. *hispidus* var. *hispidus* has been recorded for the temperate, mid eastern coast of Australia but it has the widest worldwide distribution in terms of both latitude and longitude of all the species of *Arthraxon* (van Welzen 1981). *Thelepogon australiensis* was known from only the type (**Fig. 3)** collected from northern Australia (**Map 1**). *Thelepogon elegans* has been recorded across Africa and Asia (Watson & Dallwitz 1992).

Recent curation of specimens of the Australian species of *Arthraxon* and *Thelepogon* held at the Queensland Herbarium (BRI) revealed some taxonomic anomalies. It was found that the three specimens (one sterile), of what has been previously identified as *A*. *castratus* and the holotype specimen of *T. australiensis* match each other. The three fertile specimens key to *Arthraxon* using the key to genera of grasses by Clayton & Renvoize (1986) and they key to *A*. *castratus* using the key to the species of *Arthraxon* by van Welzen (1981). However, the spikelets differ from the drawings provided by van Welzen and the type specimen of *A*. *castratus* (**Fig. 4**). Following a comprehensive study of gross morphological, micromorphological and anatomical characters (**Table 1**), it was concluded that *Thelepogon australiensis* should be transferred to *Arthraxon* and consequently the new combination *A. australiensis* (B.K.Simon) E.J.Thomps. is made below.

It was found in the process of this study that the usage of terminology in the literature for some of the characters applied to *Arthraxon*, *Thelepogon* and allies is ambiguous. Consequently, some of the terminology was re-appraised in order to enable more consistent and accurate usage (**Appendix 1)**. Defining characters and their states more precisely has potential to resolve ambiguity, aid assessment of plasticity and reliability, benefit investigations of homology and homoplasy, and provide better discrimination of taxa in alpha and beta taxonomy (Hillis 1987; Wagner 1989; Smith 1990; Lipscomb 1992; Scotland *et al*. 2003; Wiens 2004; Smith & Turner 2005).

Materials and methods

Taxon sampling

Herbarium specimens of *Arthraxon* spp. and *Thelopogon elegans* held at BRI and on loan from K, including types for *Arthraxon*, were examined. Because *A*. *castratus* has putatively the closest affinity to *A. australiensis* it was included in the detailed set of character differences presented in **Table 1**.

Plants of *Arthraxon australiensis* were cultivated in pots to study phenotypic plasticity, breeding system and to produce caryopses for future studies. The initial source of caryopses of *A. australiensis* was collected from Hammond Island in May 2016. Caryopses were scarified by scraping off a small portion of pericarp just above the scutellum. Germination was at ambient temperature on damp tissue paper in a covered transparent container in October 2016. Six plants were successfully cultivated in pots under nursery conditions in a well-drained potting medium in Brisbane, Australia (Lat. 27^0 26’ 37’’). Plants were watered daily and occasionally fertilised with a commercial pelletised chicken manure. Plants were examined in detail at flowering and fruiting during June 2017. Plants that self-propagated in pots in November 2017 and 2018 were also studied.

Fig. 3. Holotype of ***Thelepogon australiensis*** B.K.Simon (=*Arthraxon australiensis* (B.K.Simon) E.J.Thomps.), (*Clarkson 8981 & Neldner*, BRI). Image: E.J. Thompson.

Holotype of *Andropogon castratus* Griff. (= *Arthraxon castratus* (Griff.) Narayanaswami *ex* Bor.) (*Griffith 292*, K). Image: JStor Global Plants.

Lateral view of spikelet from isotype of *Andropogon rudis* Nees *ex* Steud. (= *A. castratus*) (*Siva 8837*, K). Image: E.J.Thompson.

Fig. 4. Images of ***Arthraxon castratus***.

Table 1. Morphological differences between *Arthraxon australiensis*, *A. castratus* and *Thelepogon elegans* and those considered significant in the context of subtribes of *Andropogoneae*. Data shown as {bold} are from Simon (1993); all other data in plain text was gathered by the author from herbarium specimens held at BRI. Characters and states in red are considered taxonomically significant at subtribal level.

Character		*Arthraxon australiensis*	*Arthraxon castratus*	*Thelepogon elegans*
Growth habit		geniculately ascending to 70–140 cm high, often rooting at the decumbent nodes; cultivated plants creeping with ascending inflorescence culms to 30 cm high and rooting at some nodes	geniculately ascending to 55 cm high, usually rooting at the decumbent nodes	stout, erect geniculately branching from the base with prop roots, culms to 100 cm high
Leaves	Length × width (cm)	3–13 × 0.5–1.3 {**5–12** × **0.6–1**}	1.5–5.5 × 0.6–1.0	4–18 × 0.7–2.5
	Proximal margins	ciliate with tuberculate-based erect straight simple hairs to 2.5 mm long diminishing in length towards apex of blade; small spicules to 0.25 mm long; micro-spicules to 0.15 mm long {**tuberculate-based cilia**}	ciliate with tuberculate-based erect straight simple hairs to 1.3 mm; micro-spicules *c*. 0.10 mm long; scabrid in upper 2/3 with micro-spicules to 0.2 mm long	ciliate with **spines**, 0.5–0.8 mm long; scabridulous with prickles and hooks
	Adaxial surface	sparsely hairy with erect tuberculate-based simple hairs to 1.6 mm long with medium-sized tubercle base *c*. 0.10 mm wide	sparsely hairy with erect tuberculate-based straight simple hairs to 1 mm long with small tubercle base *c*. 0.05 mm wide	sparsely hairy with two sizes of tuberculate-based erect straight simple hairs to 1.5 mm long with tubercle to 0.16 mm adjacent to the margin and to 4 mm at the margin with large tubercle base *c*. 0.20 mm wide
	Transverse section: Bulliform cells	elliptical in rows of 4–6; large, *c*. 1/2 depth of section	elliptical in rows of 3–4; large, *c*. 1/2 depth of section	elliptical in rows of 2–3; small, *c*. 1/3 depth of section
	Sclerenchyma at mid-vein	abaxial girder, oblong in outline, 3–5 cells high, as wide as vascular bundle; adaxial girder, *c*. rectangular, 3–5 cells high, narrower than bundle	abaxial girder, oblong in outline, 3–5 cells high, as wide as vascular bundle; adaxial girder, *c*. rectangular, 2 or 3 cells high, narrower than bundle	abaxial girder, linear in outline, 2 or 3 cells high, wider than bundle sheath; adaxial strand, linear in outline, 1–2 cells high
	Adaxial epidermal cells	large, *c*. 1/3 width of section section	large, *c*. 1/3 width of section	small, *c*. 1/5 width of section
Inflorescence	Type	1–3 digitate racemes arising terminally {**1–3 racemes**}	1–4 terminal digitate racemes	2–20 terminal subdigitate racemes
	Raceme length (cm)	< 6 {**2.5–5.5**}	< 3	< 10.5
	Peduncle indumentum	pilose with ascending simple hairs to 0.3 mm	pilose with ascending simple hairs to 0.7 mm long	scabrid with prickles to 0.2 mm long
Sessile spikelets	Length × width × breadth (mm)	6.7–8.9 × 1.6 × 1.5 {**6–7** × absent × **1.5**}	4.5–5 × 0.7 × 1.3–1.4	5.4–5.6 × 2.0 × 1.5
	Imbrication	*c*. 50%	*c*. 30%	0%
	Callus hair length (mm)	*c*. 1.3	*c*. 0.4	to 1.7

Table 1. continued

Glumes	Relative length of lower:upper	shorter	shorter	subequal
	Margins	*c.* 40% overlap	40–50% overlap	slightly overlapping
Lower glume	Length (mm)	6–7.3 {***c.* 6.5**}	5	5.4–5.6
	Texture	crustaceous throughout {**indurate**}	crustaceous throughout	crustaceous throughout, a little more indurated than *Arthraxon*
	Compression; transverse section shape	lateral; narrowly convex	lateral; narrowly convex	dorsi-ventral; broadly convex
	Margins	flat (not inflexed) to slightly inrolled distally, texture same as body	flat (not inflexed), texture same as body	flat, texture same as body
	Surface pattern	ridges absent; muricate with variously sized spicules, decreasing in size from top to bottom, conspicuously longitudinally; muriculate with hooks with acute to attenuate curved apices (**finely rugose**); bicellular microhairs *c.* 40 µm long, distal cell > proximal; epicuticular wax film present	ridges absent; muricate in upper half with largest spicules at the apex, longitudinally aligned; muriculate with dense covering of hooks with attenuate curved apices; bicellular microhairs *c.* 25 µm long, distal cell > proximal; epicuticular wax not observed	transversely rugose; muricate with largest spicules towards apex; muriculate with hooks with acute apices and prickles; bicellular microhairs 55–65 µm long, distal cell > proximal; epicuticular wax absent
	Venation	9 (**7**)–veined	13–veined	7–9–veined
Upper glume	Length (mm)	6.7–8.9	4.5–5.0	5.4–5.6
	Compression; transverse section shape	lateral; more or less v-shaped	lateral; more or less v-shaped	dorsi-ventral; broadly convex
	Texture	chartaceous {**coriaceous**}	chartaceous	crustaceous tapering to chartaceous towards margins
	Surface pattern	not transversely ridged	not transversely ridged	**transversely rugose** along a central longitudinal strip
	Trichomes on back	muriculate with hooks with elongated points; bi-cellular microhairs with cells about equal length	muriculate with hooks with elongated points; bi-cellular microhairs with cells about equal length	muriculate with hooks with short points; bicellular microhairs with cells about unequal, distal cell about twice length of proximal
	Margin	flat, narrowly membranous, cilia to 1.1 mm long in upper half	flat, narrowly membranous, cilia to 0.4 mm long in upper 1/3	**2-keeled**, narrowly membranous to hyaline, glabrous,
	Venation	3–veined	7–veined	3–veined
Lower floret	Composition	barren, lemma only	barren, lemma only	male, lemma and palea with 2-keeled margins
Lower lemma	Length (mm); relative to upper glume	5.0–6.7 {***c.* 4**}; *c.* ¾	3.3–3.8; ¾	5.4–5.6; sub-equal
	Texture	membranous	hyaline	hyaline
	Margins	flat, cilia to *c.* 0.5 mm long	flat, cilia to *c.* 0.4 mm long	2-keeled, glabrous

Table 1. continued

Anthers	Chasmogamous: number & length (mm)	3, 1.8 {**1.2**}	3, 1.4	CH only: both florets: 3, 3.5
	Cleistogamous: number & length (mm)	3, 1.7–2.2	3, 1.3	absent
Upper lemma	Length (mm); relative to upper glume	4.4–5.9 {***c.* 4**}; *c.* 2/3	2.2–2.5; *c.* ½	4.0–4.2; *c.* ¾
	Compression; shape of back	lateral; convex below the base of the awn and 2-keeled above	lateral; convex below the base of the awl & 2-keeled above	dorsi-ventral; convex
	Texture	membranous tapering to hyaline {**membranous**}	membranous tapering to hyaline	hyaline throughout
	Margins	flat, not winged, cilia to 0. 6 mm long	flat, not winged, cilia *c.* 0.3 mm long	flat, glabrous
	Venation	3-veined	3-veined	5-veined
	Apex	2-lobed, *c.* 1/6 of lemma length, acute	entire to minutely 2-lobed, acute	2-lobed, lobes *c.* ½ length of lemma, acute
Lower glume of pedicellate spikelet	Presence	absent or to *c.* ½ length of sessile spikelet; sterile	absent	absent
Awn	Length × width (mm); shape	14–23 × 0.3 {**< 16**}; distinctly geniculate	*c.* 7–11 × 0.1; mostly straight to slightly kinked	to 18 × 0.1; geniculate
	Column length relative to glumes	extended beyond glumes	enclosed within glumes to exserted	extending well beyond glumes
	Trichomes	appressed prickle hairs *c.* 0.05 mm long	hooks	appressed prickle hairs *c.* 0.05 mm long
	Position	**proximal**, arising 0.5 mm from base of the lemma	**proximal**, arising 0.5 mm from base of the lemma	from sinus between lobes at *c.* half total length of lemma
Pedicel	Length × width at centre (mm); relative to sessile spikelet; shape; relative to internode	3–5 {***c.* 3**} × 0.5; *c.* 2/3; linear, strap-shaped; c. as wide and as long as	1–2 × 0.2; 1/3–½; linear, strap-shaped; much narrower and shorter	7.2–11.5 × 0.8; longer; lanceolate**,** concavo-convex in TS, concavo-convex below apex; distinctly different
	Indumentum	villous on outside with ascending simple hairs *c.* 1.1 mm long increasing in length with distal ones to 2.5 mm long {**villous**}	villous on outside with ascending simple hairs 0.3–0.5 mm long increasing in length width distal ones 1.8 mm long	scabrid along veins, appressed spicules *c.* 0.3 mm long, lacking simple hairs

Table 1. continued

Callus	Width (mm); shape	0.4; circular	0.2; circular	1.2; elliptical
	Indumentum length (mm) & density	< 1.5 mm, dense	0.3–0.5, sparse	< 1.5 mm, sparse
Rachis internode	Length × width at apex (mm); relative to sessile spikelet	3.3–4.5 × 0.4–0.6; *c.* ½	3.0–3.3 × 0.3; *c.* 2/3	4.0–4.2 × 1.0–1.4; *c.* equal
	Shape; longitudinal; transverse section	capitate; narrowly concavo-convex throughout	capitate; narrowly concavo-convex throughout	distinctly clavate; concavo-convex, circular towards apex
	Texture	cartilaginous, slightly hardened	cartilaginous, slightly hardened	crustaceous
	Indumentum at apex	bearded, densely pilose with ascending hairs to 2 mm long	not bearded, sparse to medium pilose with ascending hairs to 0.5 mm long	ascending short hairs, a few cilia to 2.8 mm long on adaxial edge
	Surface	villous with ascending hairs to 1mm long	villous with ascending hairs to 0.5 – 1 mm long	distinct veination with prickle hairs
Caryopsis	Length × width × breadth (mm)	3.7–4.1 × 0.7–0.8 × 1.2–1.3 (not seen)	2.4 × 0.6 × 0.9	3.2 × 1.3 × 0.9
	Compression	**lateral**	**lateral**	dorsi-ventral
	Surface texture	longitudinally undulate, smooth	smooth	flat, finely **longitudinally striate**
	Scutellum length relative to caryopsis	< ½	< ½	*c.* 2/3

Gross morphology

The gross morphological characters and states listed in **Table 1** were obtained by observation of herbarium specimens and online images of specimens, and from descriptions, drawings and keys in the literature (Hooker 1897; Hutchinson & Dalziel 1936; Prain 1917; Clayton 1972; van Welzen 1981; Clayton & Renvoize 1986; Watson & Dallwitz 1992; Davidse 1994; Simon 1993; Simon & Alfonso 2011; Watson *et al*. 2018). Clayton (1972) listed 41 characters and states for species with an awned upper lemma in *Andropogoneae*, including *Arthraxon* and *Thelepogon*, that he used in numerical analyses but did not provide a scored matrix for character states.

Data provided in **Table 1** were gathered by observation of herbarium specimens. A range of herbarium material was examined particularly with respect to maturity of spikelets. For example, spikelets with caryopses were used for assessment of glume texture and immature material was used to observe anthers prior to anthesis. Because the veins on the upper and lower glumes were obscured by the nature of the surface texture, vein number was counted by viewing from the inside.

Micromorphology

Images of leaves and spikelets were obtained using a Nikon SMZ25 binocular microscope with a Nikon DS-Ri1 camera and images viewed using NIS-Elements BR 4.30.00 64-bit. Scanning electron microscope (SEM) images were obtained using a Phenom G2 5kev SEM with backscatter detector, and samples were prepared without sputter coating.

Leaf anatomy

Leaf transverse sections were prepared following Thompson (2017) using freehand sectioning modified from the method described by Frohlich (1984). Several sections from different BRI herbarium specimens were made for each species although only one specimen of *Arthraxon castratus* was available. Samples were rehydrated by initial immersion in hot water and soaked from a few hours to several days. Fresh material for *A. australiensis* was also sectioned. Mature leaves were chosen and sections taken from near the middle of each leaf. Leaf samples were placed on a glass slide covered with a cover slip that served as a cutting guide. Sections were cut using a razor blade while viewing under a binocular microscope at x40 magnification.

Images were obtained using a Leica DMLB compound binocular microscope with an industrial digital camera and images viewed using ToupView.

The descriptions of leaf anatomy for *Arthraxon* and *Thelepogon* by Renvoize (1982) and Watson & Dallwitz (1992) were reviewed and used as a model guide for those here.

Terminology and Nomenclature

Botanical terminology follows Harris & Harris (1994), McCusker (1999) and Beentje (2010) for general usage. Some terms for trichomes on the epidermis of grass leaves as described by Ellis (1979) are used including micro-hairs, macro-hairs, prickle hairs, angular prickle hairs and hooks. Classification of epicuticular wax follows Barthlott *et al.* (1998).

Taxonomic nomenclature is consistent with Bostock & Holland (2018) and Soreng *et al.* (2017).

Results and discussion

This study revealed differences in the following characters for the two species of *Arthraxon* and *Thelepogon*: growth habit, types of trichomes on the leaf margins, anatomy of leaf transverse sections, inflorescence type, glume compression, internode and pedicel shape and size, types of trichomes on the lower glume and surface pattern, margin of the upper glume, composition of the lower floret, position of the awn on the upper lemma, caryopsis shape and breeding system. The differences in the states of these characters for the two species of *Arthraxon* and *T. elegans* and their context in *Andropogoneae* (**Table 1)** are discussed below.

Growth habit

Plants of *Arthraxon* and *Thelepogon elegans* have distinctive differences in growth habit. *Arthraxon* species are slender, trailing to decumbent annuals or perennials usually rooting at the nodes while *T. elegans* is an annual with erect stout stems frequently with prop roots (Hooker 1897; Prain 1917; van Welzen 1981; Cope 1982; Davidse 1994). However, Watson & Dallwitz (1992) described *Arthraxon* as decumbent and *T. elegans* as erect or decumbent. A decumbent growth habit for *T. elegans* was difficult to confirm from herbarium specimens because of incompleteness of material, especially absence of lower portions of culms and bases, and insufficient label information.

Trichomes on the leaves

The various types of trichomes on the leaf margins of *Arthraxon australiensis, A. castratus* and *Thelepogon elegans* are shown in **Fig. 5.** Although both genera have ciliate margins with erect macro-hairs that consist of a transparent hair and an enlarged opaque base, they have distinctive differences. *Arthraxon* species have tuberculate-based hairs comprising a simple hair of varying length that is disjunct, at least when dry, from a somewhat donut-shaped base. *T. elegans* has trichomes with a spine-like hair confluent with an enlarged asymmetric base that is longitudinally flattened. Simon (1993) referred to these trichomes as "tuberculate-based spines". They resemble a very enlarged type of angular prickle hair as described by Ellis (1979) and are very unusual in *Andropogoneae*. They are 0.5–07 mm long whereas the typical angular prickle hairs found on most *Andropogoneae* are less than about 0.05 mm long. These spines have similarities to the trichomes on the leaf margins of some other species in *Andropogoneae* such as *Chrysopogon* Trin. (subtribe *incertae sedis*). *Chrysopogon sylvanticus* C.E.Hubb. has appressed trichomes about 0.3 mm long that also resemble very large angular prickle hairs. The homology of these apparently similar types of trichomes on the leaf margins requires further investigation (*cf.* Snow 1998).

Both genera have micro-hairs on the leaf margins. *Thelepogon elegans* has a dense covering of hooks and occasional angular prickle hairs. The *Arthraxon* species have angular prickle hairs and infrequent hooks.

On the abaxial leaf surface, the two species of *Arthraxon* and *Thelepogon elegans* have similar tuberculate-based simple hairs. All three species differ by the diameter of the tubercle and length and diameter of the hairs.

Leaf anatomy and micromorphology

Species of *Arthraxon* and *Thelepogon elegans* share the C4 photosynthetic pathway with a single bundle sheath (XyMS-) (Watson & Dallwitz 1992) as shown in transverse leaf sections of *A. australiensis*, *A. castratus* and *T. elegans* (**Fig. 6**). Differences in bulliform cells, adaxial and abaxial sclerenchyma, and adaxial epidermal cells are listed in **Table 1**.

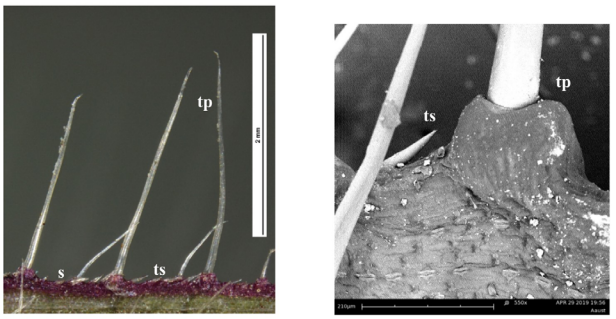
Some of these anatomical findings differ from the descriptions by Watson & Dallwitz (1992). This study found that the primary vascular bundles for *Arthraxon australiensis* and *A. castratus* have combined sclerenchyma girders, whereas Watson & Dallwitz (1992) considered this arrangement absent. *Thelepogon elegans* has adaxial strands and abaxial girders whereas Watson & Dallwitz (1992) described the sclerenchyma as combined girders.

Comparison of fresh and rehydrated sections of *Arthraxon australiensis* show overall strong similarities in anatomical characters except for radiate chlorenchyma that failed to rehydrate adequately enough for the cell pattern to be recognisable.

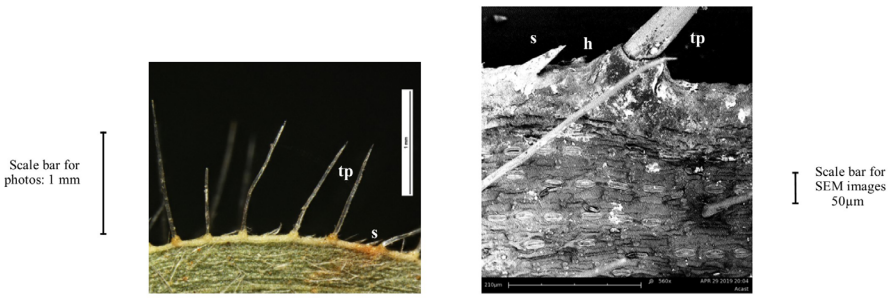
Examination of bicellular micro-hairs, stomata and silica cells from SEM for this study revealed overlapping variability across *Arthraxon* and *Thelepogon elegans*.

Inflorescences

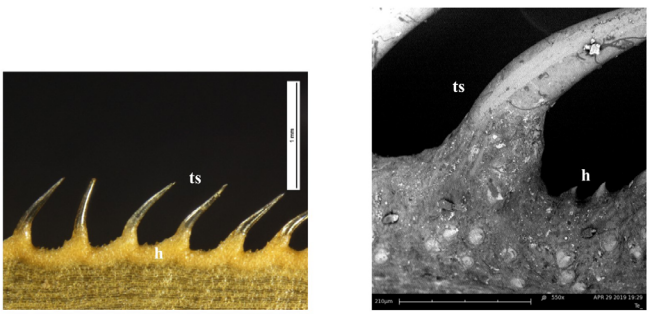
Arthraxon australiensis, A. castratus and *Thelepogon elegans* have spatheolate inflorescences but differ by the arrangement of the racemes, the longest length of racemes, the imbrication of the spikelets and the indumentum on the peduncles. *Arthraxon*



Arthraxon australiensis (both images from *Waterhouse BMW8217*, BRI)

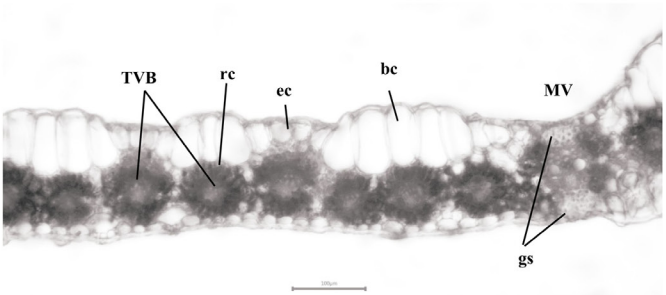


A. castratus (both images from *Simon 4231*, BRI)

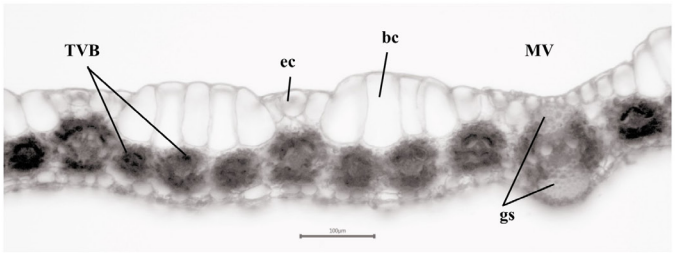


Thelepogon elegans (both images from *Burtt 5679*, BRI)

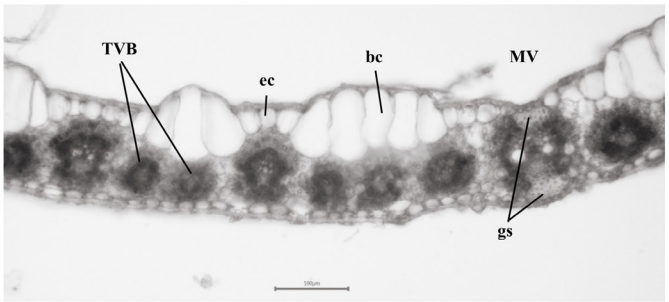
Fig. 5. Types of trichomes on the proximal margin of leaf blade using light microscopy and SEM. **tp** (tuberculate-based simple hair), **ts (**tuberculate-based spicule), **s** (spicule), **p** (prickle), **h** (hook). Images: E.J. Thompson.



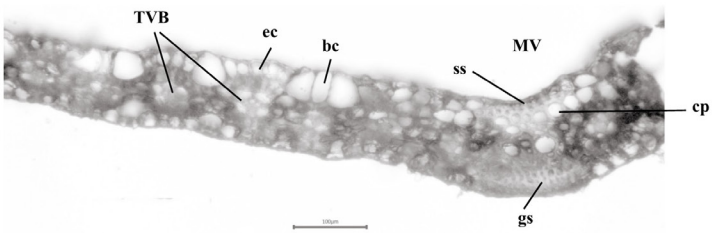
Arthraxon australiensis — from fresh material (*Thompson MOR803*, BRI)



Arthraxon australiensis — from rehydrated herbarium material (*Waterhouse BMW8217*, BRI)



Arthraxon castratus — from rehydrated herbarium material (*Simon 4231*, BRI)



Thelepogon elegans — from rehydrated herbarium material (*Gbile FH172986*, BRI)

Fig. 6. Transverse sections of leaves. All species have single vascular bundle sheaths. ***Arthraxon*** and ***Thelepogon*** differ by the bulliform cells (**bc**), shape of the girder (**gs**) and strand (**ss**) sclerenchyma at the mid vein (**MV**), and epidermal cells (**ec**). **cp** (clear parenchyma), **rc** (radiate chlorenchyma), **TVB** (tertiary vascular bundle). Scale bars on photos are 100 μm long. All images have adaxial surface upper most. Images: E.J. Thompson.

species have digitate racemes while for *T. elegans* they are mostly subdigitate and the racemes are longer. *Arthraxon* differs from *T. elegans* by the spikelets overlapping along the racemes, and the peduncles pilose with simple hairs and the latter scabrid with prickle hairs.

Sessile and pedicellate spikelets, pedicel and internode (diaspores)

Various differences occur in the composition and compression of the sessile spikelets, the relative shape and size of the rachis internode, the shape and length of the pedicel and indumentum, the presence or absence of a pedicellate spikelet, and the callus shape and size (**Fig. 7**). The lower floret of species of *Arthraxon* comprises only the lemma and is neuter. All species of *Arthraxon* lack a lower palea while *A. australiensis* and *A. castratus* are two of the three species that have an upper palea. *Thelepogon elegans* has both paleas and the lower floret male. Male lower florets are relatively uncommon in *Andropogoneae* although this character is shared by genera including *Sehima* Forssk., also placed in *incertae sedis* by Soreng *et al.* (2017), and some genera in subtribe *Rottboelliinae* Kunth. *Thelepogon elegans,* like some other *Andropogoneae* with the lower floret male, has both lower lemma and palea with 2-keeled margins.

Arthraxon species have internodes and pedicels with relatively similar structure, both more or less strap-shaped (internode slightly clavate) and *c*. half the length and much narrower than the lower glume. These structural features of the diaspore are relatively common in *Andropogoneae* while the characteristics for *Thelepogon elegans* are very uncommon. The internodes and pedicels of *T. elegans* are dissimilar with the internode conspicuously clavate and *c*. half the width and longer than the lower glume, and the pedicel longer than the internode and lanceolate in outline.

Arthraxon australiensis has incomplete pedicellate spikelets differentiated from the sessile spikelets and when present occur in upper parts of the racemes. Pedicellate spikelets are absent in *A. castratus* and *Thelepogon elegans*.

The pedicel indumentum for both species of *Arthraxon* and *Thelepogon elegans* differ in the same way as for the peduncles.

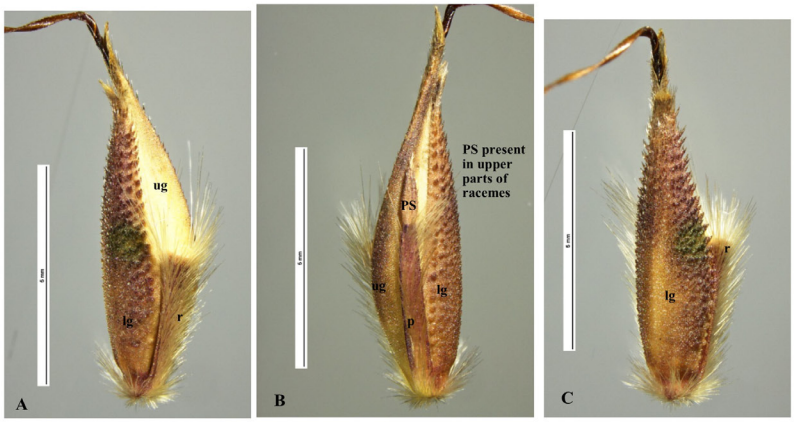
Arthraxon and *Thelepogon* differ in shape and size of the spikelet callus, the former being circular and elliptical respectively, and the latter longer.

Glumes

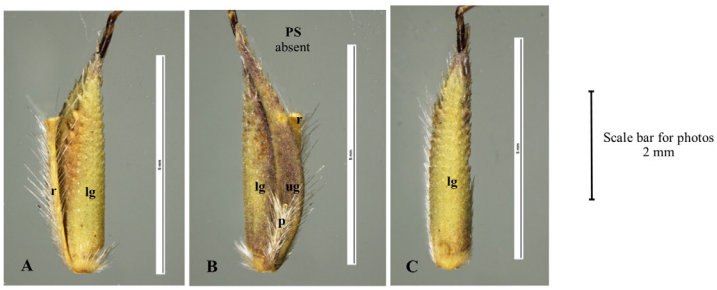
The lower and upper glumes of *Arthraxon* and *Thelepogon elegans* differ by the compression, surface texture, types of trichomes, nature of the margins, presence of epicuticular wax, and relative length. The relative compression of the lower and upper glumes differs for both genera. The glumes of *Arthraxon* are laterally compressed but strongly differentiated in transverse view, the lower glume rounded on the back and the upper glume v-shaped. Conversely, *Thelepogon* has both glumes distinctly dorsi-ventrally compressed. These two combinations of compression of the glumes for *Arthraxon* and *T. elegans* are relatively common amongst other variations in combinations of compression that can be found in *Andropogoneae*.

Arthraxon and *Thelepogon elegans* have a similar relative difference in the texture of the body of the lower and upper glumes. Both genera have the lower glumes indurated and brittle, and the upper glumes leathery to slightly hardened but pliable. Assessment of the texture of the parts of spikelets has tended to vary according to the author. The terminology used to describe the texture of the lower glume of *Arthraxon* has differed, taking into account variation between species (Prain 1917; van Welzen 1981; Clayton 1972; Clayton & Renvoize 1986; Watson & Dallwitz 1992; Simon 1993; Davidse 1994). Combinations of glumes with differentiated or similar texture occur across the genera of the subtribes of *Andropogoneae*.

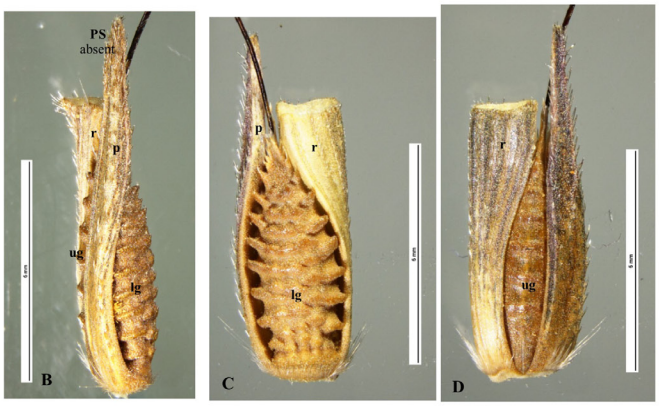
Differences in the trichomes and surface pattern on the lower glumes of *Arthraxon australiensis, A. castratus* and *Thelepogon elegans* are shown in **Figs. 8–10.** All



Arthraxon australiensis (all three images from *Thompson MOR803*, BRI)



Arthraxon castratus (all three images from *Simon 4231*, BRI)



Thelepogon elegans (all three images from *Gbile FH172986*, BRI)

Fig. 7. Perspective views of the spikelets. Differences between ***Arthraxon*** and ***Thelepogon*** include: compression of lower and upper glumes of sessile spikelet (**lg** & **ug**), shape, size and indumentum of the rachis internode (**r**) and pedicel (**p**). Scale bars on photos are 5 mm long. Views: **A** (lateral), **B** (lateral), **C** (dorsal), **D** (ventral), **PS** (pedicellate spikelet). Images: E.J. Thompson.

Arthraxon australiensis
(*Thompson MOR805*, BRI)

Upper glume margin narrowly membranous and ciliate

Arthraxon castratus
(*Simon 4231*, BRI)

Upper glume margin narrowly membranous and ciliate

Arthraxon lanceolatus* subsp. *lanceolatus
(*Mitchell 7275*, BRI)

Upper glume margin broadly hyaline and glabrous

Thelepogon elegans
(*Gbile FHI72896*, BRI)

Upper glume margin narrowly membranous and glabrous with 2-keeled margins

Fig. 8. Lateral view of the lower and upper glumes. Scale bars on images are 5 mm long. Images: E.J. Thompson.

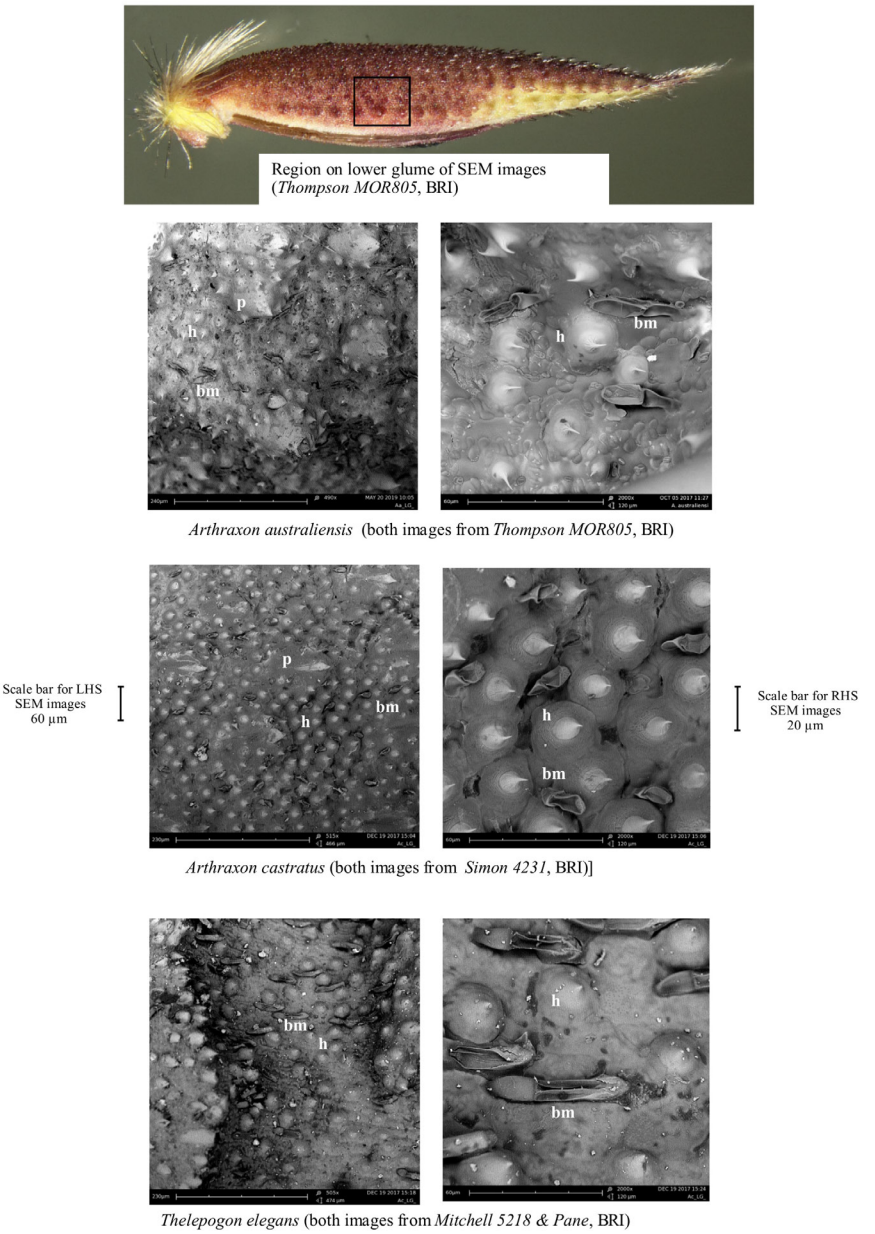
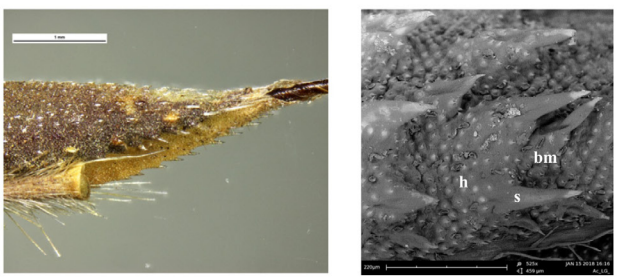
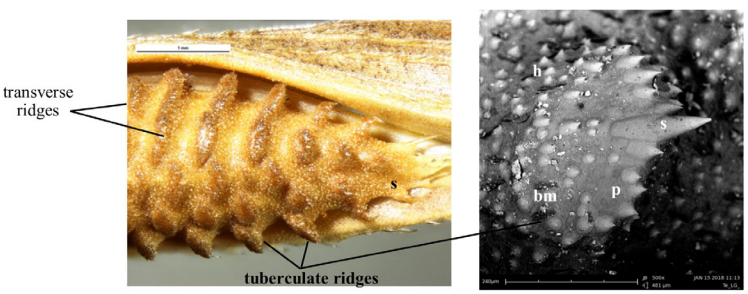


Fig. 9. SEM images at two magnifications of the surface of lower glumes showing types of trichomes and their density. ***Arthraxon*** spp. differ by the hooks (**h**) having elongated points and the bicellular microhairs (**bm**) mostly with the two cells more or less equal length and ***Thelepogon*** with the cells unequal. **p (**prickle). Images captured at *c*. ×500, LHS; ×2000, RHS. Images: E.J. Thompson.

Lateral view of *Arthraxon australiensis* showing tubercle base of spicules adorned with hooks (both images from *Thompson MOR803*, BRI)



Lateral view of *A. castratus* showing tubercle base of spicules adorned with hooks (both images from *Simon 4231*, BRI)



Dorsal view of *Thelepogon elegans* showing trichomes on transverse ridges with hooks and prickles (both images from *Gbile FHI72896*, BRI)

Fig. 10. Types of trichomes at the apex of lower glumes using light microscopy and SEM images captured at *c.* ×500. **bm** (bicellular microhair), **h** (hook), **p** (prickle), **s** (spicule). Images: E.J. Thompson.

three species have variously sized spicules increasing in length towards the glume apex. Both species of *Arthraxon* have spicules in numerous longitudinal rows and transverse ridges are absent. *Thelepogon elegans* has small spicules arising from variously discontinuous transverse ridges that occur as tubercles towards the glume apex. *Arthraxon* species have hooks with elongated arched apices and *T. elegans* has hooks with short apices as well as prickles. The characteristics of surface texture of the lower glumes of *Arthraxon* and *T. elegans* are not only dissimilar but are also distinctive in *Andropogoneae*. However, there are some broad similarities with *Jardinia* Steud. (subtribe *Rottboelliinae*).

Authors have variously applied terminology used to differentiate the surface texture of the lower glumes of genera in *Andropogoneae* (**Appendix 1**). The terminology has tended to be a mixture of categories used to describe one or the other of the two components of surface texture being the trichomes and surface patterns. It is contended here that surface texture can be assessed more consistently and definitively using separate categories for trichomes and surface patterns (**Appendix 1**).

The lower glumes of *Arthraxon australiensis, A. castratus* and *Thelepogon elegans* also differ by the presence of epicuticular wax. Film type epicuticular wax was observed on only *A. australiensis.* The lower glumes of both genera have similar bicellular micro-hairs with proximal cells shorter than the distal.

The surface texture and the margins of the upper glume of *Thelepogon elegans* have distinctive differences from *Arthraxon*. The upper glume of genera in *Andropogoneae* has usually been given little attention in descriptions although some authors used a single character such as awned, rugosity (*Thelepogon*) or number of nerves (Clayton 1972; Clayton & Renvoize 1986; Watson & Dallwitz 1992). *Thelepogon elegans* has the upper glume transversely rugose and the margins 2-keeled. Two-keeled margins on the upper glume are very rare in *Andropogoneae* but 2-keeled margins on the lower glume occur in several genera including *Ischaemum* (subtribe *Ischaeminae*), *Sehima* (subtribe *incertae sedis*) and *Thaumastochloa* C.E.Hubb. (subtribe *Rottboelliinae*). *Arthraxon* and many other genera in *Andropogoneae* have the upper glume with smooth surface pattern and flat margins. However, both genera share surfaces that are spiculate apically and muriculate with hooks although *Arthraxon* has long-pointed curved apices on the hooks and *T. elegans* has short points.

Arthraxon and *Thelepogon elegans* differ by the relative length of the lower glume to the upper glume with lower glume shorter and subequal, respectively.

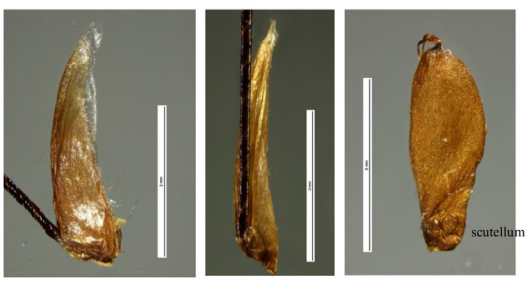
Upper lemma awn and lobes

The position of the awn, presence of lobes and compression of the upper lemma for *A. australiensis, A. castratus* and *Thelepogon elegans* is shown in **Fig. 11**. In *Arthraxon* the lobes are fused for most of their length with the awn arising near the base whereas *T. elegans* has lobes about half the length of the lemma with the awn arising at the junction. The proximal dorsal awn on the upper lemma in *Arthraxon* is unique in *Panicoideae* although it can be found in other subfamilies such as *Pooideae* Benth. (Clayton 1972; Watson & Dallwitz 1992; Watson *et al*. 2018).

Caryopsis

Caryopses of *Arthraxon australiensis*, *A. castratus* and *Thelepogon elegans* are shown in **Fig. 11**. The major differences in the caryopses relate to shape, the relative size of the scutellum and surface texture. Both species of *Arthraxon* have laterally compressed caryopses with scutellum *c*. half its length and surface smooth while the caryopsis of *T. elegans* is dorsally compressed with a larger scutellum and the surface is finely longitudinally striate. Laterally compressed and terete caryopses are very rare in *Andropogoneae* but lateral compression can also be found in *Chrysopogon*. Dorsi-ventral compression is common in the subtribes of *Andropogoneae*. Striate surface of caryopses is very rare in the tribe.

Arthraxon australiensis (all three images from *Thompson MOR803*, BRI)



Arthraxon castratus (all three images from *Simon 4231*, BRI)

Thelepogon elegans (all three images from *Gbile FH172986*, BRI)

Fig. 11. Lateral and dorsal views of the upper lemma and caryopsis. Top row left and middle, scale = 5 mm; right, scale = 2 mm. Middle and bottom rows, scale bar = 2 mm. Images: E.J. Thompson.

From examination of herbarium specimens and information published in the literature, caryopsis morphology for the species of *Arthraxon* can be divided into two groups, *viz*. terete or laterally compressed with elliptical outline in side view. In his circumscription of *Arthraxon*, van Welzen (1981) described the caryopses as "slightly ovoid-ellipsoid to cylindrical, somewhat laterally compressed" but he did not provide a description of the shape for each species. Davidse (1994) described the caryopses of *A. castratus* as "elliptic in outline, laterally slightly flattened*"*. On the other hand, Jin *et al.* (2006) described *Arthraxon* as having terete caryopses. *Arthraxon hispidus* (Thunb.) Makino, *A. lanceolatus* (Roxb.) Hochst., *A. lancifolius* (Trin.) Hochst. and *A. microphyllus* (Trin.) Hochst. have fusiform to more or less terete caryopses with smooth surface. Caryopses of *A. depressus* Stapf ex C.E.C.Fisch. and *A. jubatus* Hack. were not seen by van Welzen (1981) nor for this study.

Breeding system

The breeding systems of *Arthraxon* and *Thelepogon elegans* differ with regard to completeness of the florets of the sessile spikelets. Both genera have hermaphrodite upper florets but *Arthraxon* has the lower floret sterile while for *T. elegans* it is male.

All species of *Arthraxon* can have sessile spikelets with cleistogamous upper florets, i.e. self-fertilized within a closed flower (van Welzen 1981), but no cleistogamy has been observed for *Thelepogon elegans*. However, *Arthraxon* was not included in the respective classifications of cleistogamy in grasses by Campbell *et al.* (1983) and Culley & Klooster (2007). From herbarium specimens examined for this study, some species of *Arthraxon* had cleistogamous spikelets present. From cultivated plants, presence and abundance of cleistogamy in *A. australiensis* was found to vary within racemes and from raceme to raceme, sometimes without cleistogamous spikelets or present with low frequency. Applying the criteria presented by Thompson (2017), the type of cleistogamy found in *Arthraxon* is classified as having *monomorphic anthers on the same plants*.

Pedicellate spikelets in *Arthraxon* when present are usually sterile but in three species they are male (van Welzen 1981).

Taxonomy

Arthraxon australiensis (B.K.Simon) E.J.Thomps., **comb. nov.**; *Thelepogon australiensis* B.K.Simon, *Austrobaileya* 4: 105 (1993). **Type:** Queensland. Cook District: 62 km N of Archer River on Coen to Weipa road, 19 April 1991, *J.R. Clarkson 8981* & *V.J. Neldner* (holo: BRI [AQ570010, 2 sheets]; iso: CNS [ex MBA], K, NSW).

***Illustration*:** Simon (*loc. cit*. **Fig. 1**).

***Additional specimens examined* (all BRI): Queensland.** Cook District: Horn Island, Torres Strait, Jul 1975, *Cameron 2088*; Keriri (Hammond Island), Torres Strait, Residence in Sabatino Village, Jun 2009, *McKenna & Waterhouse SGM 562*; Keriri (Hammond Island), Torres Strait, Sabatino Village, May 2016, *Waterhouse BMW8217.* **Cultivated.** Ashgrove (ex Keriri (Hammond Island), Torres Strait, Sabatino Village), Jun 2017, *Thompson MOR805* (BRI).

***Distribution and habitat*:** *Arthraxon australiensis* is endemic to Queensland and known from Horn and Keriri Islands in Torres Strait and Cape York Peninsula (**Map 1)**. Plants have been recorded from the dense grass dominated ground layer of *Piliostigma malabaricum* (Roxb.) Benth. dominated low open woodland at the type locality, or from the banks of granite boulder strewn streams in Torres Strait islands.

***Phenology*:** Flowering and fruiting April-August.

***Affinities*:** *Arthraxon australiensis* is allied to *A. castratus* differing by the presence of pedicellate spikelets at least in the upper parts of racemes, spikelet-pairs with similar appearance of pedicel and rachis internode, and the longer lemma awn.

***Conservation status*:** The species is listed as **Vulnerable** under the *Queensland Nature Conservation Act 1992*.

***Common name*:** Cape York carpet grass.

The following key to the species of *Arthraxon* and *Thelepogon* was adapted from van Welzen (1981).

Key to the species of *Arthraxon* and *Thelepogon*

1 Upper lemma with the awn emanating from between two lateral lobes about equal in length to the lemma body; lower floret of sessile spikelet male with a palea; lower glume crustaceous, transversely rugose, ridges muricate with spicules; upper glume dorsi-ventrally compressed, transversely rugose, margins 2-keeled; caryopsis dorsi-ventrally compressed, finely striate . . . . . **T. elegans**

1. Upper lemma with a proximal dorsal awn, i.e. lobes fused except at apex; lower floret barren, reduced to a lemma; lower glume crustaceous or cartilaginous, longitudinally pectinate with spicules; upper glume laterally compressed, not ridged, margins flat; caryopsis terete to laterally compressed, smooth **2**

2 Awn < 2.3 cm long, column smooth **3**

2. Awn > 7.5 cm long, column scabridulous. . . . . **A. jubatus**

3 Glumes of sessile spikelet chartaceous on back; upper glume with broad membranous to hyaline margins *c*. half total width (**Fig. 8**); margins of lower glume inflexed to slightly incurved, wing-like; upper glume and lemmas with glabrous margins; upper palea absent; caryopsis slightly laterally compressed to terete, length/width ratio *c*. 2:1; pedicellate spikelet absent or developed; anthers 2 or 3 . . . . . **4**

3. Glumes of sessile spikelet crustaceous on back; upper glume with narrow membranous margins; margins of lower glume flat; upper glume and lemmas with ciliate margins; upper palea present; caryopsis distinctly laterally compressed, width much greater than thickness, length/width ratio > *c*. 5:1 (not seen for *A. depressus*); pedicellate spikelet absent or reduced; anthers 3. . . . . **7**

4 Pedicellate spikelet well developed **5**

4. Pedicellate spikelet absent, at least in lower parts of inflorescence **6**

5 Spikelets < 4 mm long; anthers 3 . . . . . **A. lanceolatus**

5. Spikelets > 4 mm long; anthers 2 . . . . . **A. microphyllus**

6 Pedicellate spikelets absent . . . . . **A. hispidus**

6. Pedicellate spikelets present at least in upper part of inflorescence . . . . . **A. lancifolius**

7 Spikelets with a rectangular base, crustaceous; lower glume spiculate **8**

7. Spikelets with a more or less cuneate base, chartaceous; lower glume smooth; India . . . . . **A. depressus**

8 Pedicellate spikelet present in at least upper parts of racemes; pedicel *c*. 2/3 length of rachis internode and width *c*. equal to internode; awn 14–23 mm long; Australia . . . . . **A. australiensis**

8. Pedicellate spikelet absent; pedicel much shorter and narrower than rachis internode; awn 7–11 mm long; Asia . . . . . **A. castratus**

Acknowledgements

I am very thankful to Barbara Waterhouse, Danny Mossy and Stephen Amber for herbarium specimens of *Arthraxon australiensis* and Stephen for supplying caryopses. Melody Fabillo and Gordon Guymer provided very helpful feedback on a draft of the manuscript. I greatly appreciate the helpful peer-review comments on versions of this paper by an anonymous referee and Neville Walsh.

References

Barthlott, W., Neinhuis, C., Cutler, D., Ditsch, F., Meusel, I. & Wilhelmi, H. (1998). Classification and terminology of plant epicuticular waxes. *Botanical Journal of the Linnean Society* 126: 237–260.

Beentje, H. (2010). *The Kew Plant Glossary: an illustrated dictionary of plant terms*. Kew Publishing: Royal Botanic Gardens, Kew.

Bentham, G. (1881). Notes on Gramineae. *Journal of the Linnean Society of London* 19: 14–135.

Bostock, P.D. & Holland, A.E. (2018). *Census of the Queensland Flora 2018*. http://data.qld.gov.au/dataset/census-of-the-queensland-flora-2016/, accessed 01 November 2018.

Campbell, C.S., Quinn, J.A., Cheplick, G.P. & Bell, T.J. (1983). Cleistogamy in grasses. *Annual Review of Ecology and Systematics* 14: 411–441.

Clayton, W.D. (1972). The awned genera of Andropogoneae studies in Gramineae: XXXI. *Kew Bulletin* 27: 457–474.

—— (1973). The awnless genera of Andropogoneae studies in the Gramineae: XXXIII. *Kew Bulletin* 28: 49–57.

Clayton, W.D. & Renvoize, S.A. (1986). *Genera Graminum. Grasses of the World*. Her Majesty's Stationery Office: London.

Cope, T.A. (1982). *Flora of Pakistan* No. 143 Poaceae. Department of Botany, University of Karachi: Karachi.

Culley, T.M. & Klooster, M.R. (2007). The cleistogamous breeding system: a review of its frequency, evolution, and ecology in angiosperms. *The Botanical Review* 73: 1–30.

Davidse, G. (1994). *Arthraxon*. In M.D. Dassanayake et al. (eds.), *A Revised Handbook of the Flora of Ceylon* 8: 44–49. A.A. Balkema: Rotterdam.

Ellis, R.P. (1979). A procedure for standardizing comparative leaf anatomy in the Poaceae: 2. The epidermis as seen in surface view. *Bothalia* 12: 641–671.

Frohlich, M.W. (1984). Freehand sectioning with parafilm. *Stain Technology* 59: 61–62.

Harris, J.G. & Harris, M.W. (1994). *Plant Identification Terminology: an illustrated glossary*. Spring Lake Publishing: Spring Lake, Utah.

Hillis, D.M. (1987). Molecular versus morphological approaches to systematics. *Annual Reveiw of Ecology and Systematics* 18: 23–42.

Hooker, J.D. (1897). *Flora of British India*. L. Reeve & Co.: London.

Hutchinson, J. & Dalziel, J.M. (1936). *Flora of West Tropical Africa* 2: 597. The Crown Agents for the Colonies: London.

Jin, C.S., Chen, S. & Phillips, S.M. (2006). *Arthraxon*. In W. Zhengyi, P.H. Raven & H. Deyuan (eds.), *Flora of China* 22: 616–621. Missouri Botanical Gardens Press: St Louis.

Kellogg, E.A. (2015). *The Families and Genera of Vascular Plants. Flowering Plants: Monocots: Poaceae*. Springer International Publishing AG: Cham, Switzerland.

Khan, R., Ahmad, M., Zafar, M. & Ullah, A. (2017). Scanning electron and light microscopy of foliar epidermal characters: a tool for plant taxonomists in the identification of grasses. *Microscopy Research and Technique* 80: 1123–1140.

Lazarides, M., Lenz, J. & Watson, L. (1991). *Clausospicula*, a new genus of grasses (Poaceae, Andropogoneae). *Australian Systematic Botany* 4: 391–405.

Lipscomb, D.L. (1992). Parsimony, homology and the analysis of multistate characters. *Cladistics* 8: 45–65.

Mccusker, A. (1999). Glossary. In A.E. Orchard & H.S. Thompson (ed.), *Flora of Australia: Introduction*, 2nd edition, 1: 585–636. ABRS/CSIRO Australia: Melbourne.

Nazir, A., Khan, M.A. & Shah, A. (2013). Foliar epidermal studies as an aid to the identification of grasses of tribe Andropogoneae (Poaceae) from Potohar region of Pakistan. *Pakistan Journal of Botany* 45: 235–241.

Prain, D. (1917). *Flora of Tropical Africa*. L. Reeve: London.

Renvoize, S.A. (1982). A survey of leaf-blade anatomy in grasses. I. Andropogoneae. *Kew Bulletin* 37: 315–321.

Scotland, R.W., Olmstead, R.G. & Bennett, J.R. (2003). Phylogenetic reconstruction: the role of morphology. *Systematic Biology* 52: 539–548.

Sharp, D. & Simon, B.K. (2002). *AusGrass: Grasses of Australia* (Version 1.0, June 2002). Australian Biological Resources Study: Canberra.

Simon, B.K. (1993). Studies in Australian grasses 8. A new species of *Thelepogon* (Andropogoneae: Ischaeminae) for Australia. *Austrobaileya* 4: 105–108.

Simon, B.K. & Alfonso, Y. (2011). *Ausgrass2*. http://ausgrass2.myspecies.info./, accessed 21 September 2019.

Smith, G.R. (1990). Homology in morphometrics and phylogenetics. In F.J. Rohlf & F.L. Bookstein (eds.), *Proceedings of the Michigan Morphometrics Workshop*, pp. 325–338. The University of Michigan Museum of Zoology: Michigan.

Smith, N.D. & Turner, A.H. (2005). Morphology's role in phylogenetic reconstruction: persperctive from paleontology. *Systematic Biology* 54: 166–173.

Snow, N. (1998). The use of hairs for phylogenetic inference in grasses (Poaceae). In *Monocots II: second International Conference Comput. Biol. Monocotyl. Third Intern. Symp. Grass Syst. Evol.* Abstracts, 51. Royal Botanic Gardens: Sydney.

Soreng, R.J., Peterson, P.M., Romaschenko, K., Davidse, G., Teisher, J.K., Clark, L.G., Barbera, P., Gillespie, L.J. & Zuloaga, F.O. (2017). A worldwide phylogenetic classification of the Poaceae (Gramineae) II: and update and a comparison of the two 2015 classifications. *Journal of Systematics and Evolution* 55: 259–290.

Soreng, R.J., Peterson, P.M., Romaschenko, K., Davidse, G., Zuloaga, F.O., Judziewicz, E.J., Filgueiras, T.S., Davis, J.I. & Morrone, O. (2015). A worldwide phylogenetic classification of the Poaceae (Gramineae). *Journal of Systematics and Evolution* 53: 117–137.

Thompson, E.J. (2017). *Elionurus purpureus* (*Panicoideae: Andropogoneae: Rottboelliinae*), a new species for Queensland: circumscription and breeding system *Austrobaileya* 10: 139–162.

Ullah, Z., Khan, M.A., Ahmad, M., Zafar, M. & Ullah, K. (2011). Systematic implications of foliar epidermis in Andropogoneae (Poaceae) from Hindukush-himalayas Pakistan. *Journal of Medicinal Plants Research* 5: 949–957.

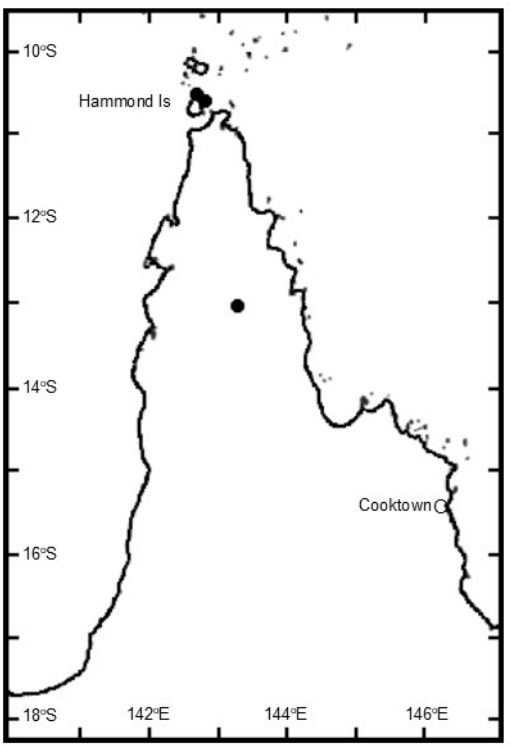
Van Welzen, P.C. (1981). A taxonomic revision of the genus *Arthraxon* Beauv. (Gramineae). *Blumea* 27: 255–300.

Wagner, G.P. (1989). The origin of morphological characters and the biological basis of homology. *Evolution* 43: 1157–1171.

Watson, L. & Dallwitz, M.J. (1992). *The Grass Genera of the World*. CAB International: Wallingford.

Watson, L., Macfarlane, T.D. & Dallwitz, M.J. (2018). *The Grass Genera of the World*. http://delta-intkey.com/grass/ident.htm, accessed 10 January 2019.

Wiens, J.J. (2004). The role of morphological data in phylogenetic reconstruction. *Systematic Biology* 53: 653–661.



Map 1. Distribution of ***Arthraxon australiensis*** based on BRI specimen point data.

Appendix 1. Terminology used by various authors to describe surface texture on the lower glume in genera in subtribes of *Andropogoneae*. Nomenclature follows Soreng *et al.* (2017)

		Subtribe/genus						
		Arthraxoninae	***Incertae sedlis***	***Ischaeminae***	***Rottboelliinae***			
Author		***Arthraxon***	***Thelepogon***	***Ischaemum***	***Jardinea***	***Hachelochloa***	***Rottboellia***	***Thaumastochloa***
Clayton & Renvoize (1986)		spinulose	rugose	rugose or not	muricate	rugose to cancellate	smooth, areolate, cancellate, rugose	smooth or rugose
Sharp & Simon (2002)		scaberulous, scabrous or rugose	scaberulous, scabrous or rugose	smooth, scaberulous, scabrous or rugose	-	rugose or latticed	-	smooth, rugulose, rugose, cancellate, longitudinally ribbed
Simon & Alfonso (2011)		rugose to prickly (sometimes with lateral rows of tubercles or spines)	strongly rugose, muricate or tuberculate	smooth, transversely rugose, tuberculate on the margins	-	lacunose, rugose	-	smooth, transversely rugose
Watson & Dallwitz (1992)		rugose to prickly (sometimes with lateral rows of tubercles or spines)	strongly rugose, or muricate, or tuberculate	smooth (rarely), rugose (transversely), or tuberculate (on the margins)	muricate to prickly	tuberculate	smooth, lacunose, rugose	transversely rugose or relatively smooth
Watson *et al*. (2016)		rugose, tuberculate, muricate, prickly	rugose, tuberculate, muricate	rugose, tuberculate	muricate, prickly	tuberculate	smooth, lacunose, rugose	smooth, rugose
This study	**Surface pattern**	without ridges	transversely rugose; tubercles ± confluent	without ridges (smooth) or rugose	without ridges	cancellate (longitudinally ribbed and transversely tuberculate); tubercles ± confluent	without ridges, longitudinally ribbed; transversely rugose; longitudinally ribbed and tuberculate in the furrows; lacunose to cancellate with longitudinal and transverse ridges (tessellate)	without ridges or transversely rugulose to rugose with ridges or longitudinally ribbed
	Trichomes	muricate to scabrid with pectinate spicules, and muriculate to scaberulous with prickles and hooks (see **Figs. 7 & 8**)	muricate to scabrid with spicules (see **Figs. 7 & 8**)	glabrous	pectinate spicules	densely muriculate with prickle hairs	glabrous	glabrous to muriculate with prickles