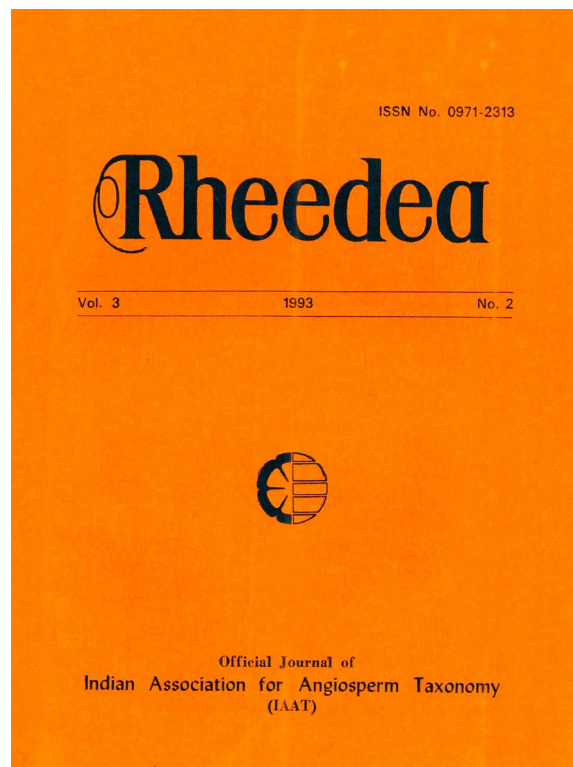




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The phylogeny of *Arthraxon* P. Beauv. (Gramineae)

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Abstract

The phylogeny of the grass genus *Arthraxon* is analyzed by applying the Wagner algorithm with parsimony. The genus *Vetiveria* has been used as outgroup. Two phylogenetic trees were found, of which one showed a trichotomy, caused by a less satisfactory optimisation on one of the characters. Therefore, the fully resolved cladogram was preferred. This cladogram comprises two groups, *A. castratus* and *A. depressus*, and the other group: *A. lanceolatus*, *A. jubatus*, *A. hispidus*, *A. lancifolius*, and *A. microphyllus*. The genus *Arthraxon* appears to be a monophyletic group within the tribe *Andropogoneae*. Typical characters are: the basal awn on the upper lemma and the subdigitate inflorescence.

INTRODUCTION

The genus *Arthraxon* comprises small grasses with procumbent branches of which the terminal parts ascend. Typical are the leaves, which are usually small, ovate, with an obcordate, subamplexicaul base, the subdigitate panicles, the laterally compressed spikelets and the upper lemma with its geniculate, subbasal awn. The spikelets break off easily and remain stuck to cloths and hair, because of the bristles on the glumes and the uncoiling, ciliate awns.

The species delimitation in the genus is quite difficult. Jain (1972), in an excellent revision of the Indian species, recognized many species and estimated that the genus would comprise more than 50 species. In my revision (Van Welzen, 1981), I only recognized 7 species, of which *A. hispidus* and *A. lanceolatus* were subdivided into 4 and 5 varieties respectively. Most of these species and varieties are also found in India. Especially *A. hispidus* is a complex species, found almost worldwide, with many locally well-recognizable forms. However, quite often forms merge in adjacent areas (e. g. the former *A. nudus* and *A. ciliaris/quarternianus* are distinct in India, but merge in S. E. Asia) or similar forms are found elsewhere (e. g., the '*A. antsirabensis*'-form from Madagascar is also found in New Guinea).

The 7 species as recognized by me form the basis of the present phylogenetic analysis. The varieties are not analysed separately, because their

ontological status is not always equal, the two wide-spread, heterogeneous type varieties have a different status than the other local, homogeneous varieties. In other words, the two type varieties are more or less paraphyletic restgroups and not monophyletic taxa like the other varieties.

The phylogenetic methodology is well explained by Eldredge & Cracraft (1980), Forey et al. (1992), and Wiley (1981). The methodology demands that a taxon should be monophyletic (all descending species of one ancestor should be included in the study), otherwise no meaningful analysis can be made. *Arthraxon* is presumably monophyletic. Clayton (1972) in a *Phenetic* analysis of the awned genera of the tribe *Andropogoneae* shows that the subtribe *Arthraxoninae* deserves a special status. Within this subtribe three groups (*Sorghastrae*, *Arthraxonastrae* and *Bothriochloastrae*) are recognized. The *Arthraxonastrae* comprise the genus *Arthraxon* only. Typical for this genus are the subdigitate inflorescence, the subbasal lemma awn, and the often greatly reduced pedicelled spikelets. Especially the first two characters indicate the uniqueness of *Arthraxon* within the *Andropogoneae* and they confirm the presumed monophyletic status of the genus.

Another prerequisite for a phylogenetic analysis is an outgroup. Preferably, this should be the sistergroup of *Arthraxon*, i. e., group of which the ancestor together with the ancestor of *Arthraxon*, share the same ancestral species. Clayton (1972) indicates that the genus *Vetiveria* in the *Sorghastrae* might be related to *Arthraxon*, because both show the unique character of laterally compressed spikelets.

PHYLOGENETIC ANALYSIS

The computer program Hennig 86 (Farris, 1989), with the characters unordered and the most elaborate tree search algorithm active, has been used to perform the analysis.

The character states for *Arthraxon* are obtained from Van Welzen (1981) and those of the genus *Vetiveria* are based on the data from a recent revision (1992) of the Malesian species by Deneewat & Yusuf (ms.). The characters used are listed in table 1.

The datamatrix is shown in table 2. The analysis of the data resulted in two equally parsimonious trees, (see fig. 1). The trees are 20 steps long, the consistency index is 0.95, and the retention index 0.90. The two phylogenetic trees only differ in the position of *A. lanceolatus*, in the cladogram shown completely its position is resolved, in the right hand cladogram (drawn partially) it shows a trichotomy with *A. jubatus* and an ancestral species. This is only a result of a different optimisation of character 1, the various alternatives are shown in fig. 1. The optimisation in the cladogram with the trichotomy is less acceptable: the

Phylogeny of *Arthraxon*

Table 1. Characters used in the phylogenetic analysis

1. Node pubescence 1=glabrous 2=glabrous to pubescent 3=pubescent	9. Lower glume margin 1=straight, small spicules 2=inflexed, broad spicules
2. Blade shape 1=linear 2=widest subbasally	10. Lower glume veins 1=not prominent 2=prominent
3. Blade base 1=linear 2=obcordate	11. Upper glume length 1=usually <4.5 mm 2=usually < 10 mm ¹
4. Inflorescence type 1=panicle 2=subdigitate	12. Upper glume awn 1=absent ² 2=often present
5. Inflorescence availability 1=free 2=subenclosed	13. Upper lemma awn insertion 1=subapical 2=subbasal
6. Joint pilosity 1=glabrous or few bristles 2=lower glabrous, upper pilose 3=all pilose	14. Upper lemma awn length 1=<<3 cm 2=>>3 cm
7. Spikelets 1=paired 2=single	15. Palea presence 1=absent 2=present
8. Glume texture 1=chartaceous 2=chitinous	16. Stamen number 1=3 ³ 2=2 ⁴
	17. Pedicelled spikelet 1=complete 2=incomplete

1 Upper glume length of many specimens of *A. hispidus* < 4.5 mm.

2 One species of *Vetiveria* with an upper glume with a short awn.

3 *Arthraxon lanceolatus* sometimes has 2 stamens.

4 *Arthraxon hispidus* sometimes has 3 stamens (var. *robustior*).

nodes have to become pilose first, after which *A. lanceolatus* partly loses the pilosity again.

The completely resolved cladogram is preferred. It shows that *Arthraxon* is distinct from *Vetiveria* in several characters (shape of the leaf blade, inflorescence, pilosity of the joints, and the attachment of the awn). Because only one outgroup was used and because the computer program always assumes that the characters of the outgroup are plesiomorphous, it is difficult to interpret which of these characters really constitute apomorphies of *Arthraxon*. However, as already

Table 2. Datamatrix of *Arthraxon* with *Vetiveria* as outgroup. ? = character state unknown, because pedicelled spikelets are absent

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
<i>Vetiveria</i>	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
<i>Arthraxon castratus</i>	1	2	2	2	1	3	3	2	1	1	1	1	2	1	1	1	?
<i>A. depressus</i>	1	2	2	2	1	3	3	1	1	1	1	1	2	1	1	1	?
<i>A. hispidus</i>	3	2	2	1	3	3	1	1	1	1	1	1	2	1	2	2	?
<i>A. jubatus</i>	3	2	2	2	2	3	1	1	1	1	1	1	2	2	2	1	1
<i>A. lanceolatus</i>	2	2	2	2	1	3	1	1	2	1	1	1	2	1	2	1	1
<i>A. lancifolius</i>	3	2	2	2	1	2	2	1	1	1	2	2	2	1	2	2	2
<i>A. microphyllus</i>	3	2	2	2	1	2	2	1	1	2	2	1	2	1	2	2	2

indicated by Clayton (1972), especially the inflorescence and the awn are unique and these characters show that *Arthraxon* is monophyletic.

Within the cladogram *A. castratus* and *A. depressus* are sister species and they are distinct from the other species. The latter forms a separate monophyletic group within *Arthraxon*. The relationships in this group can also easily be seen phenetically: *A. lancifolius* and *A. microphyllus* look very much alike, *A. hispidus* resembles them far less, and *A. jubatus* and *A. lanceolatus* look quite different.

DISCUSSION

The more or less polytypic characters (characters 11 and 16) are confirmed by the cladogram as it shows the transformations in these characters. The decrease in the glume size (character 11) is already shown by *A. hispidus* and continues in the ancestral species of *A. lancifolius* and *A. microphyllus*. The transformation from 3 to 2 stamens (character 16) is shown by both *A. lanceolatus* (mainly 3 stamens) and *A. hispidus* (mainly 2), while *A. lancifolius* and *A. microphyllus* have only 2 stamens.

At least one species of *Vetiveria* (*V. filipes*) shows an upper glume with a short awn (character 12). However, because the whole genus *Vetiveria* was characterized in the matrix, this was not coded separately. The cladogram shows that the possession of a glume awn is a separate, parallel development in *Vetiveria* and in *A. lancifolius*. A similar convergence can be found in the absence of a lemma awn in *V. zizanioides* and in several specimens of *A. hispidus*.

If the species concept of Jain (1972) is applied, then the phylogenetic tree (fig. 1) shows where the additional species have to be appended, and *A. lanceolatus* and *A. hispidus* will be at the base of two monophyletic subtrees of species. *A. lanceolatus*, for instance, shows two distinct transformation series, one is to have broad-based spicules on all veins of the lower glume (a series from var. *lanceolatus* to var. *echinatus*) and the other series shows a development towards more hairs

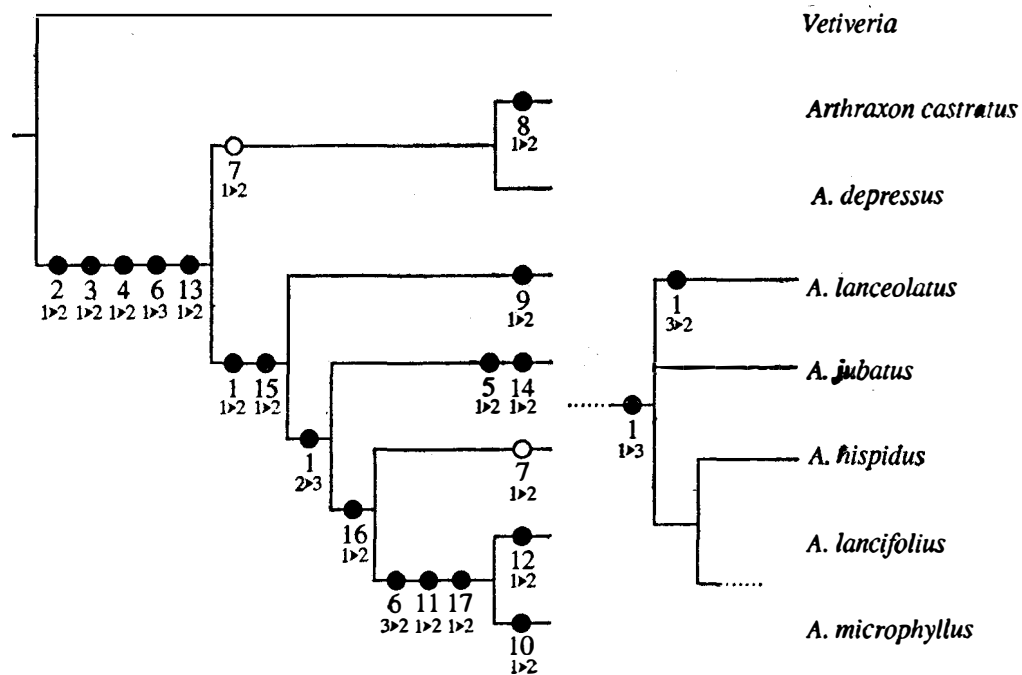


Figure 1: The Phylogeny *Arthraxon*. Two equally parsimonious phylogenetic trees were found. One is completely resolved (left) and selected as the accepted cladogram; the other shows a trichotomy (right, partly shown) and is rejected, also because of a less preferred optimisation of character 1. ● = apomorphy, ○ = parallelism.

per broad-based spicule on the marginal nerves of the lower glumes, together with a unification of these spicules into wings and an increase in the pilosity of the lower glume (a series from var. *lanceolatus* through var. *meeboldii*, to var. *raizadae* to var. *villosus*). In *A. hispidus* less obvious series are present, there seems to be a series towards increase in size of either the spikelets (var. *hispidus* to var. *santapau*) or of the whole plant (var. *hispidus* to var. *robustior*), and a series towards a decrease in size, especially of the spikelets (var. *hispidus* to var. *junnarensis*).

Once the phylogeny of a taxon is known, the data can be combined with the distribution of the taxa and a historical biogeographic analysis can be made. However, such an analysis is useful only when the taxon studied can be compared with other (independent) taxa and when the taxa have limited distribution. The latter condition is absent in most species of *Arthraxon*. *A. hispidus*, *A. lanceolatus*, and *A. lancifolius* are very widespread, from Africa to India, S.E. Asia, parts of Malaysia to sometimes Australia. *A. hispidus* is also known from central and north America. *A. castratus* has a more limited distribution; it is present in India, S. E. Asia, and Java. Only *A. depressus*, *A. jubatus* (both S. India), and *A. microphyllus* (N. E.

India to N. Thailand) show limited distribution. Moreover, in historical biogeography usually vicariance is assumed. *Arthraxon*, especially with its widespread species, shows mainly dispersal: it is introduced in America and it can only have spread over Malesia via dispersal as Malesia is, tectonically, of Australian origin. Therefore, no historical biogeographic analysis could be attempted.

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