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REVIEW ARTICLE

A Review on the Genus *Isachne* R. Br. (Poaceae) - Taxonomic evaluation and recent updates for the species from Kerala, India

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Abstract

The genus *Isachne* includes grasses which are found particularly in wetlands. Most of the species included in the genus are either endemic or rare, one of the exception being *Isachne globosa,* which is found in almost all regions from where the other species have been reported. Their rarity and diminutive florets make it difficult for taxonomists to identify, collect, distinguish and microscopically study them. The most available grass *I. globosa* can be used as a representative species and is well flourished in regions where they grow. Also, it shows intraspecific variations, which again makes taxonomists hard to distinguish the species. Recently *I. henryi* reported in 1988 has been shown to be a variation of *I. globosa.* No taxonomic studies or revisions have been carried out in this genus so far. The present study targets review of the genus which also highlights observations of the present researchers. An extensive study of the genus is recommended to unwind the existing taxonomic ambiguities.

Keywords

Endemic; florets; grass; Isachneae; Micrairoideae; spikelets

Introduction

Poaceae or Gramineae is the fourth largest angiosperm family and contains approximately 12000 grass species in nearly 800 genera worldwide. The distribution of grasses is open and frequent. They can be found on any continent including Antarctica. Grasses are extremely successful in planet-wide distribution due to their highly reduced floral structure and wind pollination mechanisms. Vegetative propagation through rhizomes and stolons as well as the enormous growth facilitated by intercalary meristems permit their luxuriant growth.

The most important characteristic of this family is the one-seeded indehiscent fruit known as caryopsis (grain), which is rich in starchy endosperm. Morphologically, grasses consist of a stem termed culm, fibrous roots, parallel-veined leaves with a blade (upper portion) and cylindrical sheaths (lower portion), as well as primary inflorescence referred to as spikelets. A spikelet has one or more, two ranked bracts inserted along the rachilla. Each spikelet has two lower bracts called glumes, above which pairs of bracts known as florets are born. Each floret consists of a lower bract known as lemma and an upper bract, palea. Within each palea, inconspicuous flowers can be found.

The subfamily Micrairoideae has been subjected to intense modifications since it was established by Pilger (1). This was due to the misplacements of its

genera, regarding their morphologies (2), anatomy (3), physiology and phylogeny (4, 5) The subfamily is characterized by grasses with alternate or whorled leaves, bisexual spikelets articulated above the glumes, cartilaginous or coriaceous lemma and palea; linear hilum and starchy endosperm (5). The spikelets of Micraroideae grasses have two florets, which are usually bisexual except in some species (*Micraira, Isachne, Sphaerocaryum* and *Limnopoa*) which has a proximal sterile floret or staminate one. According to Lazarides (6), most species of the subfamily are mat forming, with a few caespitose and some decumbent. So far, all taxa have a fringe of hairs as ligule. All taxa of the subfamily tend to have small embryos in their caryopsis, except some of the species with either long-linear (*Eriachne, Isachne, Limnopoa, Micraira* and *Pheidocloa*) or a short linear hilum (*Coelachne, Heteranthoecia* and *Sphaerocaryum*). Also, the endosperm has simple (panicoid-type) starch grains. The members of the subfamily share a similar pattern of habitat and distribution, ecologically. They are found typically in mesophytic, swamps, wet areas or near coastal areas, but may occur in inland areas as well. Rarely, some species are found in xerophytic habitats (5).

Genus *Isachne* R. Br., included in the subfamily Micraroideae, within the tribe Isachneae Benth., comprises of approximately 100 species distributed worldwide (7, 8). The distribution of *Isachne* R.Br. is in tropical and subtropical regions of the world. Though the highest number of species occur in tropical and temperate Asia, some species also come about in Africa, America, Pacific Islands and Australia (9, 10, 11). The infrageneric classification of *Isachne* is still doubtful and under dispute. In the neotropical region, *Isachne* is the only representative, comprising of annual or perennial grasses, usually with slender or stout, erect or decumbent culms (9). In India, the genus is represented by 31 species, out of which 14 species have been reported from Kerala.

Morphology

The genus *Isachne* includes annual or perennial grasses. Iskandar and Veldkamp had made a brief account on the morphology of the genus *Isachne* in general terms. They found the presence of glandular bands on the culms below the nodes and on the branches of the inflorescences. Also, that the longer pedicel had glandular bands while the shorter ones are not glandular. The spikelets are bi-flowered and dehisce above the glumes. They found that almost all Panicoid species generally dehisce as a whole with the glumes (except *Icananthus* P. Beauv.). As an important characteristic of the Panicoideae, they suggested that the spikelets are abaxial. But this cannot be taken into account now as *Isachne* has been included historically in Panicoideae but presently in the Micraroideae. Iskandar and Veldkamp also suggested that *Isachne* can have spikelets with both florets bisexual, the plesiomorphic condition, while they also suggested that the situation might be inconstant. In their study, they concluded that in one of the species (*Isachne villosa*), the lower floret is male, while in other five species, the upper one was female i.e., *I. brasii, I. diabolica, I. globosa* (the upper one was rarely bisexual), *I. minutula* and *I. pulchella.* The upper floret was always bisexual in *I.langkawiensis* and *I. villosa* (12).

Currently, *Isachne* is included in the tribe *Isachneae* and is divided according to the degree of similarity of anthecia- *Isachne* sect. *Isachne* includes species with heteromorphic anthecia (dissimilar anthecia) while *Isachne* sect. *Albens* V. Prakash and S.K. Jain includes species with homomorphic anthecia (similar anthecia) (13).

Description

Annuals or perennials. Culms erect to decumbent, climbing or leaning, creeping or stoloniferous, sometimes tufted, ribbed or robust, branching and rebranching at top; nodes glabrous, sometimes sparsely to densely tuberculate hairy with or without glandular bands in between, generally rooted at lower nodes; internodes long, ribbed, glabrous, sometimes hollow, expanded at the base; leaf blade ovate to ovate-lanceolate, linear-lanceolate or ovate to elliptic rounded, amplexicaul or not amplexicaul, rounded to subcordate at base, apex acute, sometimes cartilaginous and scabrid, margins thick, ciliate or scabrous, nerves 10-28, prominently raised, sparsely to hirsute on nerves above, sparsely hirsute below; ligules if present ciliate; panicles many flowered, branched, with or without glandular bands; panicles 2-18 cm long, branched with or without glandular bands, smooth, glabrous to minutely scabrous spikelets, densely flowered; peduncle more or less ribbed, 8-26 branches; spikelets 1-2.3x1-1.2 mm long, globose-ovoid, elliptic-globose to oblong, ovate-elliptic or ellipsoid, glabrous; glumes subequal, similar or dissimilar in size and shape; lower glume ovate- elliptic, obtuse, elliptic-lanceolate or ovate lanceolate, mostly obtuse at apex, 5-11 nerved, sometime caducous at or after anthesis, margins hyaline, pale, greenish-purple or purplish; upper glumes ovate-orbicular, obtuse, rounded, obovate to elliptic-obovate or ovate-lanceolate, apex acute or rounded to emarginated, mostly chartaceous, 3-8 nerved, margins hyaline, green-purple, green-hyaline , greenish or purplish, sometimes few sentose hairs on dorsal side; florets mostly 2, homomorphic or heteromorphic anthecia; lower anthecia bisexual, pistillate or staminate, ovate-elliptic or oblong to elliptical, apex obtuse or rounded to subacute; lower lemma 0.8 × 1.2 mm, ovate or ovate-elliptic, apex rounded to subacute, chartaceous, mostly 5-nerved, sometimes longitudinally grooved, glabrous or inconspicuously puberulous (bicellular microhairs); lower palea mostly flat, ovate-elliptic, elliptic, or ovate-elliptic, margins incurved, glabrous or sparsely puberulous, obtuse at apex; rachilla extension ca. 0.1 mm long, inconspicuous between florets, glabrous, flat; upper lemma plano convex, ovate elliptic or oblong to elliptical, mostly 7 nerved, sometimes puberulent throughout, incurved margins; upper palea flat or ovate, mostly obtuse at apex, subcoriaceous, glabrous or sparsely pubescent; lodicules 2, membranous, hyaline; stamens 3, filaments 0.1-0.2 mm long, anthers 0.6-1.5 mm

long, oblong, creamish to brownish; stigma 2, plumose, purplish; caryopsis 0.2 - 1 x 0.1 - 0.8 mm , oblong, brownish to black.

Phylogenetics and Classification

The first species referable to *Isachne* appears to be pre-Linnaean *Meneritana Gramen miliaceum folio hirsuto* (the classical Greek name for *Panicum miliiaceum*) by Hermann (14). It was later mentioned informally by Linnaeus. In the course of time, it has been identified as *Isachne globosa* (Thunb.) Kuntze. *Meneritana* was never mentioned again by Linnaeus in any of his publications or in his Species Plantarum. Thunberg described *Milium globosum* from Japan, which was the basionym of *I. globose* (15). Later, *Isachne* with a single species *I. australis* R.Br. was set up by Brown, remarking that *Meneritana* Herm. belonged to the same genus (16). However, *I. australis* also turned out to be a synonym of *I. globosa.*

Roemer and Schultes included *Meneritana* in *Neurachne* R.Br. (17) and added three species from Roth's 'Novae Plantarum Species' to *Isachne* (18). Sprengel dusted four species of then known *Isachne* throughout his concept of *Panicum* L (19). So, Sprengel seemed to be the first to formally associate both the genera- *Isachne and Panicum.* Trinius mentioned *I. miliaceae as* the existing species and added three new species - *I. atrovirens* (Trin.) which was a synonym of *I.globosa., I. rigens* (Sw.) Trin., and *I.panicea* Trin (20). He added two more species - *I.albens* Trin. and *I.dispar* Trin (21). Later Kunth reported 7 species, the first among which was to be reported from the New World was *Isachne dubia* Kunth. which was a superfluous name for *Panicum dispermum* Lam. = *I.disperma* (Lam) Doell (22). Kunth reported 3 more species and in 1833, the list came up to be 10 (23).

The genus *Isachne* was placed in *Panicum by* Steudel in 1840 (24). Doll placed *Isachne* after *Panicum* (25). Bentham included *Isachne* in the subtribe *Milieae* of his 'Poaceae' (26) but in 1881, he recognised *Isachneae* as a distinct tribe, following the views of General Munro. Bentham also distinguished the taxon *Panicaceae* (27) , which is now regarded as misplaced (12). By describing the pubescence of spikelets, Hooker f. suggested that *Isachne* belongs to Poaceae (28). Subsequently, Hackel placed the genus next to *Panicum* (29). Chase conferred the history and relationship of the genus. She differentiated *Isachneae* against *Heteranthoecia* Stapf (30). Stapf made a subtribe with alternative names *Isachnastae* and *Isachninae* in the *Paniceae* which also included *Isachne* and *Heteranthoecia* (31).

Hitchcock revised 8 species of American origin, with regard to the position inconsistency in the *Paniceae* due to the structure and division of sexuality of the spikelets (32). Camus added the genus in *Paniceae* (33) while Pilger included *Isachne* in the subtribe *Panicinae* (1). Hubbard removed *Isachneae* from the *Paniceae* (34). Potztal conducted extensive studies on anatomy on the representative genera included by Hubbard. She found festucoid leaf anatomy and concluded that majority of the *Isachneae* should be placed in *Panicoideae* (3). Janseng gave a survey of 36 Malaysian taxa (35). Pilger accepted Bentham's tribe in the *Panicoideae* since his student Portzal had concluded so (36).

Metcalfe, by studying anatomy of leaf of some species, concluded that the leaf structure of the genus *Isachne* would be of panicoid, but of a unique type. The uniqueness was due to the presence of acutely angled silica bodies, long narrow mesophyll cells and cubical long cells, which was found especially in *Isachne* and other related genera of *Isachneae*. He also found that the radiate mesophyll (*Isachne*-type) was also found in many C_3 *Paniceae* (37). In 1960, Bor retained the tribe in *Pooideae* (38). Jacques-Felix placed the *Isachneae* next to *Paniceae* (39). The treatment by Pai-Chieh (40), as reported by Iskandar and Veldkamp, accepted *Isachninae* as a distinct subtribe in *Paniceae* (12).

Based on leaf anatomy and photosynthesis, Brown proposed an evolutionary strategy for *Panicea.* He considered *Isachne* as modern descendants of the 2-fertile -floret, non-Kranz, pre-Paniceae stage of evolution (41). The Indian representatives of the genus were studied and published as a revision by Prakash (42). Following the floristic treatments of Bor (38), they recognised 29 species for *Isachne*. Prakash and Jain presented a description of phytogeography of the tribe and a survey of the leaf anatomy. They recognized 110 species for *Isachne* with speciation centres in India and Malaysia, so they have thought that the origin of *Isachne* might be there (43). Most of the taxa mentioned for Africa are synonymous with *I. buettneri* or not *Isachne* at all (12). Kellog and Campbell found that *Isachneae* and *Panicoideae* have a sister relationship and suggested that *Isachneae* might be polyphyletic (44).

Soreng and Pennington found the subtribe *Isachninae* synonymous to *Isachneae*, and included in *Panicoideae* (45). Iskander and Veldkamp studied the history of genus and published a revision of Malaysian *Isachne*, thus providing a key to identify the different species then reported in the genus (12). Later molecular studies became popular and generated rbcL + ndhF sequences (46) and Sanchez- Ken and Clark generated ndF + rpl16 intron sequences for some the genera including *Isachne* and a more structured PACCAD clade (Panicoideae + Arundinoideae + Centothecoideae + Chloridoideae + Aristidoideae + Danthonioideae) with strong support for each subfamily. They also included *Isachne* R.Br. in *Panicoideae* (5).

A hypothesis was put forward that *Isachne* and *Eriachne* might be more closely related to each other than either is to *Micraira*, as they share some spikelet characters. It was also suggested that these characters were homoplastic, since they shared a panicoid core and that this was one of the reasons that both genera were misclassified in the subfamily Micraioideae in different tribes by most authors. *Isachne* was included in Micraioideae within the PACCAMAD clade (2, 4, 27). A team by Duvall also supported that *Isachne* and *Eriachne* as sister taxa in all their analyses (46). The results of

molecular studies in 2011 supported the genus *Isachne* as monophyletic. This is against the report of *Isachneae* being non-monophyletic due to the inclusion of both the genera *Isachne* and *Coelachne* in it (44).

While conducting molecular studies by a team led by Bouchenak, they experienced difficulties in the inclusion of *Isachne* in Micraroideae or the PACCMAD clade and suggested that the subfamilial position of the genus is unclear. They also reported monophyly of Eriachneae + Micraireae group, but excluded *Isachne* (47). A worldwide phylogenetic classification of the Poaceae was made by some researchers in 2011. They placed *Isachne,* along with *Coelachne*, *Heteranthoecia*, *Limnopoa* and *Sphaerocaryum* in the tribe *Isachneae* Benth. [1881] (syn. - subtribe Isachninae Stapf [1898]) of the subfamily Micrairoideae. They updated it in the same year by comparing it to their first classification and expanded the tribe *Isachneae* by including *Isachne, Coelachne*, *Heteranthoecia, Sphaerocaryum and Hubbardia.* They also reported that *Isachnae* was by far the largest tribe in the subfamily and was required a worldwide revision as *Isachne* was portrayed as paraphyletic by many authors (48). *Isachne* R.Br. and *Coelachne* R.Br. were described as the most diverse genera in the tribe *Isachneae*. According to them, *Isachne* belongs to Micrairoideae, the subfamily included in the PACMAD clade (Panicoideae + Aristidoideae + Chloridoideae + Micrairoideae + Arundinoideae + Danthoioideae) (7). Grasses in this clade have been taxonomically revised and require the application of improved tools for a better understanding of the relationships.

Genus *Isachne* in the Indian Scenario

105 species of *Isachne* is reported worldwide (Table 1). It is interesting to note that out of the 31 species of *Isachne* reported from India, approximately 70% can be found in South India, specifically in Karnataka, Kerala and Tamil Nadu. This may be due to the availability of numerous wetlands and a specific climatic condition. Among them, *I. deccanensis* and *I. oreades* are endemic to Tamil Nadu while *I. mysorensis* is endemic to Karnataka. *I. mysorensis* reported in 1971 by Sundararaghavan has been rediscovered after 44 years from a locality other than the type locality. The species has been rediscovered from Mookambika Wildlife Sanctuary, Karnataka. It is assigned critically endangered status (49).

Among the 14 species reported from Kerala (Table 2), *I. bhatii, I. edamalayarensis, I. fischeri, I. jayachandranii. I. kannurensis* and *I. manilaliana* are endemic to Kerala. It is clear that the state hosts most of the rare and endemic species of the genus. *I. veldkampii* K. G. Bhat and Nagendran with its type locality in Karnataka has been recorded newly from Kannur district of Kerala (50). 10 species has been reported from Maharashtra, the west zone of India. Among them, *I. bicolor, I. borii* and *I. swaminathanii* are endemic to the state. All of the three species are found in altitude ranging from 600-1000 m above sea level.

The north-east zone of India is home to *I. sylvestris* which is endemic to Assam (Barak Valley), *I. kinabaluensis* reported from Assam and Khasi Hills of Maghalaya and *I. clarkei* from Lachung, Sikkim and Kohima, Nagaland. Also, *I. sikkimensis* and *I. dimyloides* are reported from Sikkim. They are reported to be found at an elevation ranging from 500m to 1800m. *I. himalaica* is reported from both north-east and northern India. It is distributed in Assam, Kashmir, East and West Himalayas and found in damp places along stream beds at an elevation 1000-1500 m. Another interesting species is *I. confusa* whose native range is Java, Sumatra and Nicobar Islands of India. According to the authors, its short leaf sheath, minute ovate and pilose leaves and tiny spikelets make it distinct from all other species of the genus (51).

I. globosa, I pulchella and *I. albens* are found to be widely distributed and occupy most of the states in the country. Extremely wide distribution is shown by *I. globosa*. It was the first species to be reported from the genus and many of the species and varieties once reported as new have been synonymised to *I. globosa* due to misidentifications. So it is clear that the species shows intraspecific variations. Except the aforesaid three widely distributed species and some of the species such as *I. bhatii, I. kannurensis* and *I. veldkampii* reported from the lateritic plateau of Kerala (about 49m altitude), all other species occupy a habitat of elevation ranging from 500 m to 3000 m.

Contribution of Taxonomists for Indian species of the Genus

Majority of species of *Isachne* in India were discovered during the 19th and 20th century, a time period where there was a shortage of taxonomists of Indian origin. Most of the taxonomists were foreign born who explored Indian vegetation either out of curiosity or as a part of their jobs. Carl Benhard von Trinius (1778-1844) was a German botanist and physician. As a botanist, Trinius was a specialist in grasses and described many species included in the genera *Agrostis, Cinna*, *Isachne, Paspalum, Aeluropus* and *Apera* in his book Fundementa Agrostographiae during the time period 1820-1841. He described *Isachne albens* and *I. dispar* during this period. Later, *I. dispar* was reported as a synonym of *I. globosa.* Robert Wight (1796-1872) spent much of his life in India between 1819 and 1853 and mostly devoted himself to the study of flora of Indian Peninsula. He was appointed in charge of Botanical establishment at Madras in 1826. He made extensive collection trips to the virgin forests of South India (52). He proposed two species of *Isachne* from India - *I. kunthiana* and *I. walkeri.*

Cecil Ernest Claude Fischer (1874-1950) was the Divisional Forest Officer in 1909 in Forest Research Institute, Dehradun. He became the assistant for India in Kew Herbarium (1925-1937) and did the most valuable works including the completion of Gamble's unfinished Flora of Presidency Madras. He has provided critical publications under "New or little known plants from South India" during the period 1932 to 1940 in the Kew Bulletin. (53). It was during this period, Fischer would have

Table 1. *Isachne* spp. distributed worldwide

	Taxon	Native Range	Year of publication
1.	*Isachne pulchella* Roth	Tropical and Subtropical Asia to Marianas	1817
2.	*I. rigens* (Sw.) Trin.	Guatemala, Caribbean, Venezuela to Peru	1826
3.	*I. albens* Trin. (*Isachne albens* var. *hispidula* (Hack.) Veldkamp)	Tropical and Subtropical Old World	1827
4.	*I. mauritianana* Kunth	Tropical Africa, W. Indian Ocean	1830
5.	*I. minutula* (Gaudich.) Kunth	Tropical Asia to N. Australia	1831
6.	*I. myosotis* Nees.	Nansei-shoto to SE.China, Indo-China to N. Australia	1850
7.	*I. pangerangensis* Zoll. & Moritzi	Malaysia	1854
8.	*I. kunthiana* (Wight & Arn. ex Steud.) Miq.	India, Sri Lanka	1857
9.	*I. elegans* Dalzell	India to Myanmar	1861
10.	*I. leersioides* Griseb	Cuba	1862
11.	*I. arundinaceae* (Sw.) Griseb.	Mexico to Tropical America	1864
12.	*I. pygmaea* Griseb.	Jamaica	1864
13.	*I. walkeri* (Arn. ex Steud.) Wight & Arn. ex Thwaites	SW. India and S. India	1864
14.	*I. disperma* (Lam.) Doll	Lesser Antilles to Trinidad	1877
15.	*I. polygonoides* (Lam.) Doll	S. Mexico to Tropical America	1877
16.	*I. multiflora* (Thwaites) Ferguson	Sri Lanka	1880
17.	*I. distichophylla* Munro ex. Hillebr.	Hawaiian Islands, Cook Islands	1888
18.	*I. pallens* Hillebr.	Hawaiian Islands	1888
19.	*I. comata* Munro ex. Hack.	New Caledonia to Vanuatu	1889
20.	*I. cochinchinensis* Balansa	Indo-China	1890
21.	*I. globosa* (Thunb.) Kuntze	Oman, Tropical and Subtropical Asia to W. Pacific	1891
22.	*I. cernua* C. Cordem	Reunion Island (Indian Ocean)	1895
23.	*I. longifolia* C. Cordem.	Reunion Islands	1895
24.	*I. clarkei* Hook. f.	E. Himalaya to Taiwan and New Guinea	1896
25.	*I. himalaica* Hook. f.	Afghanistan to Myanmar	1896
26.	*I. lisboae* Hook. f.	W.India, SW. India, Vietnam	1896
27.	*I. scabrosa* Hook. f.	Nepal to Tibet and Myanmar	1896
28.	*I. angolensis* Rendle	Nigeria to S. Tropical Africa	1899
29.	*I. schmidtii* Hack.	Indo-China to Papuasia	1901
30.	*I. angustifolia* Nash	Puerto Rico to Lesser Antilles	1903
31.	*I. rigidifolia* (Poir.) Urb.	Caribbean	1903
32.	*I. sylvestris* Ridl.	Assam to China (Fujian, Guangdong)	1905
33.	*I. stricta* Elmer	Philippines to New Guinea	1908
34.	*I. vitiensis* Rendle	Vanuatu, Fiji	1909
35.	*I. vulcanica* Merr.	Philippines (Negros: Mt. Canlaon)	1910
36.	*I. truncata* A.Camus	S. China to Vietnam	1912
37.	*I. clementis* Merr.	W. Malesia	1917
38.	*I. kinabaluensis* Merr.	Assam to W. Malaysia	1917
39.	*I. chevalieri* A. Camus	Vietnam	1919
40.	*I. eberhardtii* A. Camus	Vietna	1919
41.	*I.commelinifolia* Warb.	SE. China to Indo-China, Japan (S.Kyushu) to Taiwan	1920
42.	*I. ciliaris* B. Boivin ex. A. Camus	Madagascar (E. Africa)	1927
43.	*I. gracilis* C.E.Hubb	India	1927
44.	*I. vaughanii* C.E.Hubb	Mauritius, Reunion Islands	1927
45.	*I. petelotii* A. Camus	Vietnam	1928
46.	*I. brassii* Hitchc.	Sulawesi to New Guinea	1929
47.	*I. angladei* C.E.C. Fisch.	S. India (Tamil Nadu)	1932
48.	*I. bourneorum* C.E.C. Fisch `	SW. India	1932
49.	*I. kiyalaensis* Robyns	W&W. Central Tropical Africa	1932
50.	*I. meeboldi* C.E.C. Fisch	SW. India (Karnataka, Maharashtra)	1932

51.	*I. setosa* C.E.C. Fisch	SW. India and S. India	1932
52.	*I. gossweileri* Stapf & C.E.Hubb	Angola (S.Africa)	1933
53.	*I. guineensis* Stapf. & C.E.Hubb.	Guinea	1933
54.	*I. nipponensis* Ohwi	S.China to Korea, S. Central and S. Japan, Taiwan.	1935
55.	*I. ascendens* Swallen	Vietnam	1936
56.	*I. dioica* Swallen	Vietnam	1936
57.	*I.carolinensis* Ohwi	Solomon Islands to Caroline Islands	1941
58.	*I. arfakensis* Ohwi	New Guinea to N. Vanuatu	1942
59.	*I. ligulata* Swallen	W. America and N. America	1943
60.	*I. confusa* Ohwi	SE. China to Indo-China and NW. Pacific	1947
61.	*I. diabolica* Bor	W. Sumatera	1947
62.	*I. muscicola* A. Camus	Madagascar	1947
63.	*I. trachycaula* Ohwi	N. Sumatera	1947
64.	*I. villosa* (Hitchc.) Reeder	Papuasia	1948
65.	*I. deccanensis* Bor	India (Tamil Nadu)	1949
66.	*I. dimyloides* Bor	Darjeeling to Assam	1949
67.	*I. fischeri* Bor	S W India	1949
68.	*I. humicola* A. Camus	Madagascar	1949
69.	*I. sikkimensis* Bor	Central and E. Himalaya to Tibet	1949
70.	*I. pubescens* Swallen	S. Mexico to Honduras	1950
71.	*I. humbertiana* A. Camus	Madagascar	1952
72.	*I. langkawiensis* Jansen	NE. Thailand and Peninsular Malaysia (Langkawi)	1953
73.	*I. smitinandiana* A.Camus	Indo-China	1953
74.	*I. surgens* Jansen	Sulawesi (Mt. Bonthain)	1953
75.	*I. lutchuensis* Hatus. & T. Koyama	Nansei-shoto (Iriomote-jima)	1956
76.	*I. oreades* (Domin) Bor	India (Tamil Nadu)	1960
77.	*I. ciliatiflora* Keng f.	Sichuan (China)	1965
78.	*I. hainanensis* Keng f.	China (Guangdong) to Hainan	1965
79.	*I. hoi* Keng. f.	China (Guangdong, Hunan, Zhejiang)	1965
80.	*I. puberula* Bor	Thailand	1965
81.	*I. cambodiensis* Ohwi	Cambodia	1967
82.	*I. borii* Hemadri	W. India (Maharashtra)	1971
83.	*I. mysorensis* Sundararagh.	SW. India	1971
84.	*I. bicolor* Naik & Patunkar	W. India (Maharashtra)	1976
85.	*I. swaminathanii* V.Prakash & S.K. Jain	W. India	1983
86.	*I. veldkampii* K.G. Bhat & Nagendran	SW. India (Karnataka)	1983
87.	*I. guangxiensis* W.Z.Fang	China (Fujian, Guangxi, Hong Kong)	1984
88.	*I. salzmannii* (Trin. ex Steud) Renvoize	Brazil (Bahia)	1984
89.	*I. goiasensis* Renvoize	Brazil (Goias, Brasilia D.F.)	1987
90.	*I. henryi* S.R.Sriniv. & Sreek.	India (Kerala)	1988
91.	*I. jayachandranii* Gopalan & V. Chandras	India (Kerala)	2000
92.	*I. homonyma* Veldkamp	Reunion Islands	2004
93.	*I. stenantha* (Steud) Veldkamp	Madagascar	2004
94.	*I. venusta* Veldkamp	Reunion Islands	2004
95.	*I. sharpii* B.K.Simon	NE. Queensland	2010
96.	*I. hirtiglumis* Longhi-Wagner & Welker	Brazil (Minas Gerais)	2014
97.	*I. kannurensis* Sunil, Ratheesh, Sujana & Sreek.	India (Kerala)	2014
98.	*I. albens* var. *buettneri* (Hack.) Veldkamp	Tropical Africa	2016
99.	*I. bhatii* P. Biju, Josekutty & Augustine	S. India (Kerala)	2016
100.	*I. edamalayarensis* Sunil, Naveen Kum. & Sivad..	India (Kerala)	2016
101.	*I. manilaliana* Sunil, K.M.P. Kumar & V.P. Thomas	India (Kerala)	2017
102.	*I.bsipiana* Veldkamp	Vanuatu	2018
103.	*I. fera* Veldkamp	Sumatera	2018
104.	*I. glandulosa* Veldkamp	Sumatera	2018
105.	*I. soderstromii* R.S. Rodrigues & Filg.	Dominica	2018
106.	*I. burchellii* R.S. Rodrigues & Filg.	Brazil (Rio de Janeiro)	2019
107.	*I. veldkampii* var *malabarica* V.S.A. Kumar, Dhanya & P. Biju	India (Kerala)	2022

Table 2. *Isachne* spp. in Kerala

	Species	Reported location in Kerala	Year of report
1	*Isachne pulchella* Roth	Kollam	1817
2	*I. kunthiana* (Wight & Arn. ex Steud.) Miq.	Idukki	1857
3	*I. walker* (Arn. ex Steud.) Wight & Arn. ex Thwaites	Idukki	1864
4	*I. globosa* (Thunb.) Kuntze	Throughout Kerala	1891
5	*I. gracilis* C.E. Hubb	Palakkad	1927
6	*I. bourneorum* C.E.C. Fisch `	Idukki	1932
7	*I. setosa* C.E.C. Fisch	Idukki, Wayanad	1932
8	*I. fischeri* Bor	Idukki	1949
9	*I. veldkampii* K.G. Bhat & Nagendran	Kasaragod	1983
10	*I. jayachandranii* Gopalan & V. Chandras	Agasthyamalai	2000
11	*I. kannurensis* Sunil, Ratheesh, Sujana & Sreek.	Kasaragod	2014
12	*I. bhatii* P. Biju, Josekutty & Augustine	Kasaragod	2016
13	*I. edamalayarensis* Sunil, Naveen Kum. & Sivad..	Edamalayar Forest Range	2016
14	*I. manilaliana* Sunil, K.M.P. Kumar & V.P. Thomas	Muthikulam, Palakkad	2017
	I. veldkampii var *malabarica* V.S.A. Kumar, Dhanya & P. Biju	India (Kerala)	2022

described four species of *Isachne* in the year 1932 - *I. angladei, I. bourneorum, I. meeboldi* and *I. setosa* from South India .

Norman Loftus Bor (1893-1972) was an Irish botanist. He was the assistant director of Kew Gardens from 1948-59. He has worked on the grasses of Assam (1938), Flora of Assam (1940) and Manuals of Indian Botany (1953). He dealt with taxonomy of Indian plants and ecology of Assam and Nilgiris. In particular, he concentrated on the study of grasses and in 1949, he described *Isachne deccanesis* and *I. fischeri* from Nilgiris, *I. dimyloides* from Assam and *I. sikkimensis* from Sikkim.

Charles Edward Hubbard (1900-80) was a British botanist specialised in grasses. He was considered as the master of classification and recognition of grasses. *Isachne gracilis* collected by Meebold in 1927 was verified and described by Hubbard. Naik (1933-2012) and Patunkar were angiosperm taxonomists of India. Naik completed the Flora of Marathwada (1980). He is the author of Taxonomy of Angiosperms (1984) and described *Coelachne ghatica* (1980). Out of the three grass species described by Naik and Patunkar, one of them was *Isachne bicolor* reported in 1976. (54).

Sudhanshu Kumar Jain (1926-2021) is known as the 'father of ethnobotany'. He was interested in floristics, plant taxonomy and biodiversity conservation. Along with his student Ved Prakash, he discovered *I. swaminathani,* an endemic grass from Maharashtra in 1983 during Prakash's research work on grasses (55). Veerichetty Chandrasekharan born in 1941 is an Indian taxonomist who proposed a number of species from Tamil Nadu. Among them was *I. jayachandrani* reported in the year 2000. Hemadri Koppula was an employee of Botanic Survey of India who contributed 24 species and one genus to the world flora. He described *Isachne borii* from Maharashtra in 1971.

Kakunje Gopalakrishna Bhat (1947-2022) was one of the well-known taxonomists in India. He started his doctoral studies in 1980 on the topic 'Studies of sedges and grasses of Coorg and South Kanara districts of Karnataka'. It would be during this period, Bhat and Nagendran came across *I. veldkampii* reported from Karnataka in 1983. He established a Taxonomy Research Centre in Udupi. (56). Sunil, Naveen and Sivadasan described *I. edamalayarensis* from the Western Ghats of Kerala. Sivadasan and Sunil detailed the Flora of Alappuzha district of Kerala in 2009.

Distribution of the genus in Kerala

The species of *Isachne* discovered from Kerala dates back to the 19th century, the oldest species reported being *I. pulchella* (1817), *I. kunthiana* (1857), *I. walkeri* (1864) and *I. globosa* (1891). The non-availability of scientific technology during those periods had definite impacts on the descriptions and illustrations of the above mentioned taxa. Most of the data regarding florets and its parts such as palea and lemma are either non-clear or lacking. On the contrary, recent discoveries such as *I. kannurensis* (2014), *I. manilaliana* (2017) and *I. veldkampii* var. *malabarica* (57) have clear cut taxonomic data sufficient enough to distinguish these species with more clarity. Available herbaria of the species reported from Kerala are provided (Figures 1-3). A detailed study and in depth morphological analysis is necessary to resolve the confusions that exist in the genus.

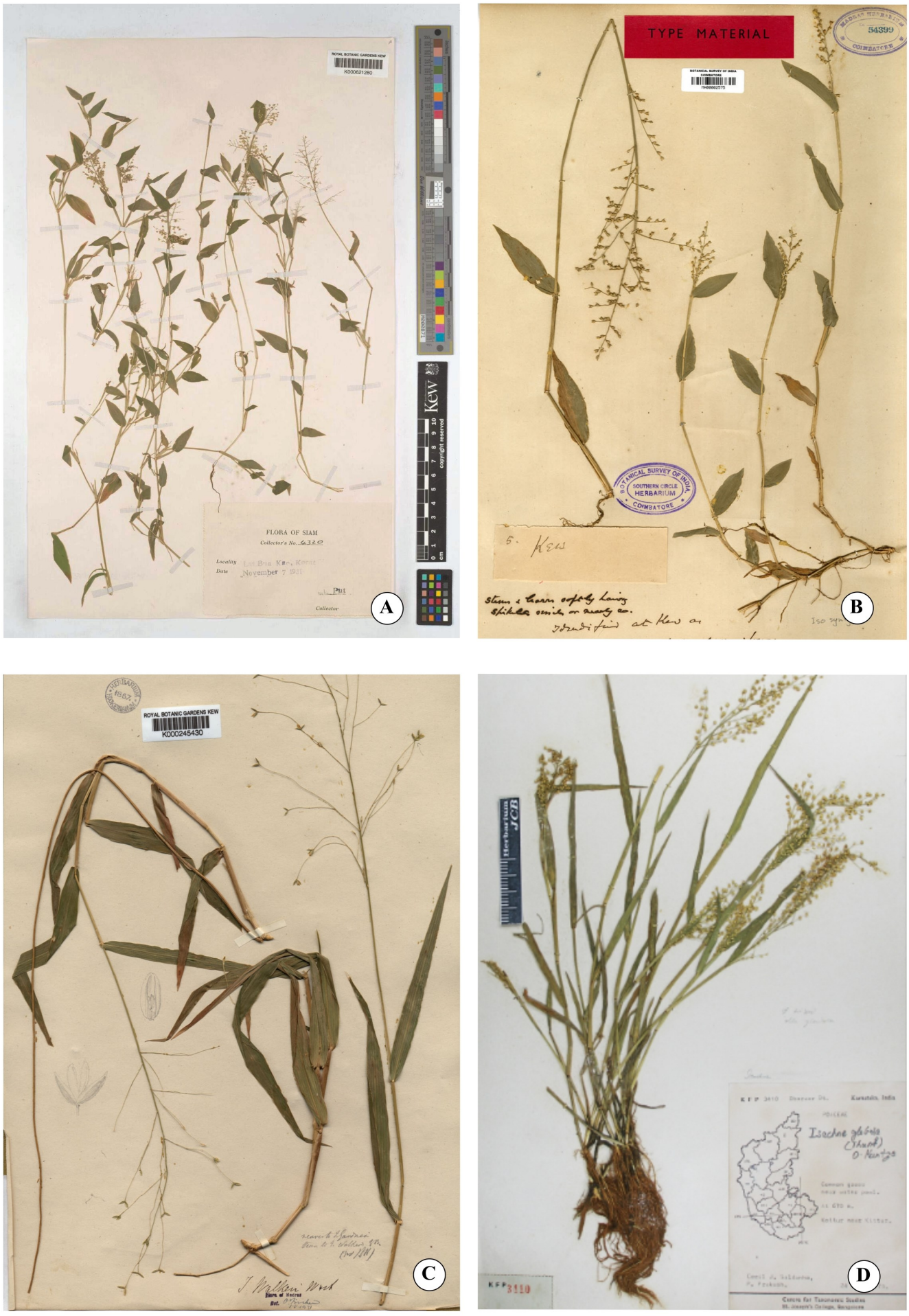

Figure 1. Herbarium Specimens. A, *Isachne pulchella*; B, *I. kunthiana*; C. *I. walkeri*; D, *I. globosa*

Figure 2. Herbarium Specimens. A, *Isachne gracilis*; B, *I. bourneorum*; C, *I. setosa*; D, *I. fischeri*

Figure 3. Herbarium Specimens. A, *Isachne veldkampii*; B, *I. jayachandranii*; C, *I. kannurensis*; D, *I. edamalayarensis;* E, *I. manilaliana.*

Most recently, *I. henryi,* a species reported from Wayanad district of Kerala during 1988 has been recognised as a misidentification. *I. henryi* shows overlapping traits with *I. globosa.* Dhanya and Anil Kumar (58) concluded that the high degree of phenotypic plasticity shown by *I. globosa* might have led Srinivasan and Sreekumar to wrongly identify it as a novel one at that time (59).

A key has been provided making use of the existing data for the identification of species in Kerala.

1a. Nodes bearded ……2

1b. Nodes glabrous ……3

2a. Prostate or creeping decumbent culms…… Isachne pulchella

2b. Erect or geniculately ascending culms……4

3a. Glumes dissimilar……5

3b. Glumes similar……6

4a. Leaves lanceolate, up to 6 mm long…… *I. fischeri*

4b. Leaves ovate or lanceolate, 1-3(-6) mm long…… 7

5a. Lower floret staminate; upper floret pistillate; lower glume 5-nerved; upper glume 7-nerved…….. *I. edamalayarensis*

5b. Lower floret staminate; upper floret pistillate or bisexual lower glume 5-7 nerved; upper glume 7-11 nerved…… *I. globosa*

6a. Pedicels with glandular bands……8

6b. Pedicels without glandular bands…… 9

7a. Panicle linear and cylindrical, racemes appressed along central axis; spikelets 3.2-3.7 mm long…….. *I. manilaliana*

7b.Panicle open and effuse, racemes lax; spikelets 2-3(-4) mm long…… 10

8a. Culms rambling and mat forming, woody; leaves lanceolate; lower glume 7-9 nerved …… *I. walkeri*

8b. Culms erect, slender, leaves ovate, cordate; lower glume 3 -nerved…… 11

9a. Leaves linear-lanceolate, 2.5-6.5 cm long; panicle branches glandular; lower glume 3-nerved…… *I. bhatii*

9b. Leaves ovate, 0.75-4 cm; panicle branches eglandular; lower glume 5-nerved…… *I. gracilis*

10a. Leaves ovate or ovate-lanceolate, 1-3 cm long; panicles up to 5 cm long…… 12

10b. Leaves lanceolate or elliptic or ovate, 1-6 cm long; panicles 2-12 cm long…… 13

11a. Culms 12-40 cm long; panicles 2-8.5 cm long; upper glume 3-5 nerved…… *I. kannurensis*

11b. Culms 3-8.5 cm long; panicles 0.7-2 cm long; upper glume 5-nerved…… *I. veldkampii*

12a. Culms 3-18 cm long; spikelets 2-3 mm long; glumes dissimilar; lower glume 5-nerved; upper glume 7-nerved…… *I. setosa*

12b. Culms up to 50 cm long; spikelets 2-4 mm long; glumes similar; lower glume 7-nerved; upper glume 7-nerved…… *I. jayachandranii*

13a. Leaves amplexicaul; spikelets 2-3.5 mm; lower glume 5 -nerved; upper glume 7-nerved…… I. *kunthiana*

13b. Leaves not amplexicaul; spikelets 3-4 mm; lower glume 7-9 nerved; upper glume 5-7 nerved…… *I. bourneorum*

Conclusion

No studies of the genus have been carried out since the report of a variety, *Isachne veldkampii* var *malabarica* (57). The last report of a novel species in the genus was in 2019 from Brazil, which is *I. burchelli* (60). The above mentioned authors work specifically on the genus which might help them to distinguish the grass species which otherwise is a strenuous task. Most of the species in the genus are either rare or endemic, which makes it difficult to collect the plants for further studies. Micromorphological or molecular studies in the genus are completely lacking.

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Authors' contributions

PALD conducted the literature survey and initially drafted the manuscript. VSAK corrected and finalised the review article. Both authors have reviewed and approved the final manuscript.

Compliance with ethical standards

Conflict of interest: The authors declare that they have no conflicts of interest.

Ethical issues: None.

References

1. Pilger R. Gramineae III. Die naturlichen Pflanzenfamilien., (2nd edn); 1940.
2. Clayton WD, Renvoize SA. Genera graminum. Grasses of the world. Grasses of the World. 1986; 13: 1-389
3. Potztal E. Über die blattanatomie der Isachneae. Botanische Jahrbücher für Systematik, Pflanzengeschichte und Pflanzengeographie. 1952; 75: 551-69.
4. GRASS PHYLOGENY WORKING GROUP, Barker NP, Clark LG, Davis JI, Duvall MR, et al. Phylogeny and subfamilial classification of the grasses (Poaceae). Annals of the Missouri Botanical Garden. 2001; 373-57. https://doi.org/10.2307/3298585

5. Sanchen-Ken JG, Clark LG, Kellogg EA, Kay EE. Reinstatement and emendation of subfamily Micrairoideae (Poaceae). Systematic Botany. 2007; 32(1): 71-80. https://doi.org/10.1600/036364407780360102
6. Lazarides M. The genus Eriachne (Eriachneae, Poaceae). Australian Systematic Botany. 1995; 8(3): 355-52. https://doi.org/10.1071/SB9950355
7. Duvall MR, Yadav SR, Burke SV, Wysocki WP. Grass plastomes reveal unexpected paraphyly with endemic species of Micrairoideae from India and new haplotype markers in Arundinoideae. American Journal of Botany. 2017; 104: 1-10. https://doi.org/10.3732/ajb.1600285
8. Soreng RJ, Peterson PM, Romaschenko K, Davidse G, et al. A worldwide phylogenetic classification of the Poaceae (Gramineae) II: An update and a comparison of two 2015 classifications. Journal of Systematics and Evolution. 2017; 55 (4): 259-90. https://doi.org/10.1111/jse.12262
9. Renvoize SA. A new Isachne (Gramineae) from Brazil. Kew bulletin. 1987; 42(4): 927-28. https://doi.org/10.2307/4109938
10. Judziewicz EJ. Family 187. Poaceae (Gramineae). A. Gorts-van Rijn (ed.), Flora of the Guianas, Series A, Phanerogams. 1990; 8: 1-727.
11. Clayton WD, Vorontsova MS, Harman KT, Williamson H. 2006 onwards. GrassBase - The online world grass flora. http://www.kew.org/data/grasses-db.html
12. Iskandar EA, Veldkamp JF. A revision of Malesian Isachne sect. Isachne (Gramineae, Panicoideae, Isachneae). Reinwardtia. 2003; 12(2): 159-79.
13. Veldkamp JF. New status and combinations for the two East African taxa of Isachne R. Br. (Gramineae). Botany Letters. 2016; 163(1): 19-24. https://doi.org/10.1080/12538078.2015.1127772
14. Hermann, P. Musaeum zeylanicum 24. 1717
15. Thunberg CP. Flora japonica. 1784.
16. Brown R. Prodromus Florae Novae Hollandiae Johnson & Soc., London. 1810; 1: 196.
17. Roemer JJ, Schultes JA. Systema vegetabilium. 1817; 2: 475-76.
18. Roth AW. Alberti Guilielmi Roth: Novae plantarum species praesertim Indiae orientalis. sumptibus H. Vogleri; 1821
19. Sprengel K. Rondeletia glomerulata. Caroli Linnaei, Systema Vegetabilium, editio decima sexta 1; 1824.
20. Trinius CB, 1820. Fund. Agrost. i-x. J. G Heubner, Viennae.
21. Trinius CB. Species Graminum Iconibus et Descriptionibus: Academia Imperialis Scientiarum St. Pétersburg 85-86; 1828. https://doi.org/10.5962/bhl.title.15525
22. Kunth CS. Révision des Graminées: 46, 49. Gide fils, Paris. 1829.
23. Kunth C. Enumeratio plantarum 1: 136-37. Cottae, Stuttgart, Tübingen. 1833.
24. Steudel EG. Nomenclator botanicus. 1840; 2(1): 823.
25. Doll JC. Gramineae I. Oryzeae, Phalarideae, Paniceae In: C.F.P. Martius (ed.). Flora Brasiliensis Enumeratio Plantarum: 358; 1877.
26. Bentham G. Flora Australiensis. 1878; 7: 457.
27. Bentham G. Notes on Gramineae. Journal of Linnaean Society Botany. 1881; 19: 30.
28. Hooker JD. Flora of British India 7: 25. L. Reeve & Co. 1896.
29. Hackel E. Gramineae. Die Naturlichen Pflanzenfamilien 2: 70-89. 1887.
30. Chase A. Notes on genera of Paniceae. IV. Proceedings of Biological Society of Washington. 1911; 24(106): 149-51.
31. Stapf O. Gramineae. Prain, D. Flora of tropical África. 1917; 9: 13-16.
32. Hitchcock AS. The North American species of Isachne. Contributions from the United States National Herbarium. 1920; 22(3): 115-21.
33. Camus A. (camus EG, Camus A). Graminées. In F. Gagnepain, Flore générale del'Indo-Chine Masson & Cie, Paris. 7: 409-18; 1922.
34. Hubbard CE. Limnopoa meeboldii (CEC Fischer) CE Hubbard. Hooker's Icones Plantarum, 1-4. 1943.
35. Jansen P. Notes on Malaysian grasses-I. Reinwardtia 2: 279-92. 1953.
36. Pilger R. Das system der Gramineae. Botanishe Jahrbucher fur Systematik. 1954; 76: 281-84.
37. Metcalfe CR. Anatomy of the monocotyledons. 1. Gramineae. Anatomy of the monocotyledons. 1. Gramineae 257-62. 1960.
38. Bor NL. The grasses of Burma, Ceylon, India and Pakistan (excluding Bambusae) International Series of monographs on pure and applied botany. 1960; 547: 576-83.
39. Jacques Felix H. Les graminées (Poaceae) d'Afrique tropicale. 1. Généralités, classification, description des genres. IRAT. BulletinScientifique. 1962; 1: 262-64.
40. Pai Chieh Keng. Revision of the genus Isachne R. Br. (Gramineae) of China. Acta Phytotaxonomica Sinica. 1965; 10(1): 6-24.
41. Brown WV. The Kranz syndrome and its subtypes in grass systematics. Memoirs of the Torrey Botanical Club 1-97; 1977.
42. Prakash V. Poaceae-tribe-Isachneae. Fascicle of Flora of India. 1984; 14: 7-37.
43. Prakash V, Jain SK. On the phytogeography of the tribe Isachneae (Poaceae). Journal of the Indian Botanical Society. 1987; 66(1-2): 107-15.
44. Kellogg EA, Campbell CS. Phylogenetic analyses of the Gramineae. In International Symposium on Grass Systematics and Evolution, Washington, DC (USA), Smithsonian Institution Press. 310-22. 1988.
45. Soreng RJ, Pennington SJ. Catalogue of New World grasses (Poaceae): III. Subfamilies Panicoideae, Aristidoideae, Arundinoideae and Danthonioideae. The Contributions from the United States National Herbarium 46: 273. 2003.
46. Duvall MR, Davis JI, Clark LG, Noll JD, et al. Phylogeny of the grasses (Poaceae) revisited. Aliso: A Journal of Systematic and Evolutionary Botany. 2007; 23(1): 237-47. https://doi.org/10.5642/aliso.20072301.18
47. Bouchenak-Khelladi Y, Salamin N, Savolainen V, Forest F, et al. Large multi-gene phylogenetic trees of the grasses (Poaceae): progress towards complete tribal and generic level sampling. Molecular phylogenetics and evolution. 2008; 47(2): 488-05. https://doi.org/10.1016/j.ympev.2008.01.035
48. Soreng RJ, Peterson PM, Romaschenko K, Davidse G, et al. A worldwide phylogenetic classification of the Poaceae (Gramineae): phylogenetic classification of the grasses. Journal of Systematics and Evolution. 2015; 53:117-37. https://doi.org/10.1111/jse.12150
49. Singh Rajeev. New distributional record of Isachne mysorensis sundararagh - an endangered grass from mookambika wildlife sanctuary, karnataka, India. Indian Forester. 2015; 141: 223-24.
50. C. Pramod, Pradeep AK. Isachne veldkampii (Poaceae) a new record for Kerala, India. 2012; 36. 59-61.
51. Ohwi J. Bulletin of the National Science Museum, Tokyo. 1947; 18: 14.
52. Basak RK. Robert Wight and His Botanical Studies in India. Vol. 30. Wiley. 1981; 4: 784-93. https://doi.org/10.2307/1220080

53. Rajan R, Vivekananthan K. Contributions of J.S. Gamble and C.E.C Fischer to the Flora of Erstwhile Madas Presidency. Bull. Bot. Surv. India. Vol 22. 1-6. 1981. https://doi.org/10.20324/nelumbo/v23/1981/74899

54. Patunkar BW. Grasses of Marathwada. Scientific Publishers, Jodhpur. 1980.

55. Vartika Jain, Anil KG. Notable Contributions of Dr. SK. Jain to Floristics, Plant Taxonomy, Phytogeography and Conservation 19.3-13. 2019.

56. Ningaraj KK, Shreyas B. Orbituary: Kakunje Gopalakrishna Bhat. Rheedea. 2022; 32(2): 139-40. https://doi.org/10.22244/rheedea.2021.32.02.07

57. Dhanya PAL, Biju P, Kumar VSA. Isachne veldkampii var. malabarica (Poaceae) - a new wetland variety from Northern Kerala, India. Plant Science Today 2022; 9 (sp1): 29-32. https://doi.org/10.14719/pst.1678

58. Dhanya PAL, Kumar VSA. Revising the taxonomic status of Isachne henryi S.R. Sriniv. & Sreek. (Poaceae) Feddes Repertorium 2024; 00: 1-7.

59. Srinivasan SR, Sreekumar PV. Isachne henryi, a new species of Poaceae from Kerala, India. Journal of the Bombay Natural History Society. 1988; 84(3): 647-49.

60. Rodrigues RS, Filgueiras TS. *Isachne burchellii* (Poaceae, Micraioideae) from Rio de Janeiro, Brazil - an endemic new species segregated from Isachne goiasensis. Brittonia. 2019. 71 (3), 242-52. https://doi.org/10.1007/s12228-019-09576-x