An Updated Overview of Taxonomy and Phylogenetic History of Tillandsioideae Genera (*Bromeliaceae: Poales*)

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Abstract: Generic delimitation in Tillandsioideae has been widely discussed over the last past decades, being frequent changes in generic level. Despite the numerous changes at the generic and infrageneric levels in Tillandsioideae there is not yet a study bringing together the history of systematic of the tillandsioid genera. Given the conservation significance and scientific importance of species of the subfamily, it is time revise the generic status of Tillandsioideae. Therefore the purpose of this paper is to provide an updated phylogenetic and systematic history for the genera of Tillandsioideae. We review the fragmentary literature on the phylogeny, classification and taxonomy of Tillandsioideae, and provide an update of these data.

Keywords: Bromeliads, classification, monocots, monophyletic, polyphyletic.

INTRODUCTION

Bromeliaceae Juss. (Poales) is a morphologically distinctive and ecologically diverse family from the New World. In the current sense is estimated that there are 3248 species in 58 genera [1], in the Neotropical region, with the exception of *Pitcairnia feliciana* (A. Chev.) Harms & Mildbr., a single taxon outside from American continent, native of the west Africa, in the region of Guinea [2, 3].

Recognized the high degree of adaptive radiation [4], bromeliads has great importance for conservation biology, due to the high rate of endemism in many of its species, but is also recognized for its ecological, economic, physiological and ornamental importance [5, 6].

In the Americas, the species occurs from southern North America, through Central America to Patagonia (Argentina) almost in the meridional extreme of South America. The main centers of diversity and endemism are located in coastal line of Brazil, occupied by the luxuriant Atlantic Forest, the hottest-spot biome where 31 genera, 803 species and 150 infraspecific taxa are registered [7], and the region of Venezuelan Tepuis [8].

Among the monocots, Bromeliaceae stand out as one well-supported family [9], morphologically distinct by following features: (1) capability of trichomes in absorbing water and nutrients (peltate scales), (2) stigma conduplicate-spiral [10, 11], and (3) basic number of 25 chromosomes, except in *Cryptanthus* with 17-18, and rarely in few species of Tillandsioideae and Bromelioideae [12, 13]. However, issues of systematics, on its evolutionary pattern, especially concerning to taxonomic delimitation of genera and species, have received constant criticism [11, 14, 15].

Historically the family has been divided into three major groups: Pitcairnioideae, Tillandsioideae and Bromelioideae, mainly in accordance with habit, position of the ovary and morphology of fruits and seeds [2, 8, 16]. Early phylogenetic studies [10, 17] corroborated with the classical taxonomy, indicating the monophyly of the three subfamilies. With the advances of molecular analyses, most taxa and different regions of the genome were gradually being included and the monophyly of the subfamilies challenged. In the last four decades the three subfamilies have been extensively studied and their relationships discussed. Several phylogenetic studies using morphological and molecular data have been performed to understand the relationships among and within subfamilies [6, 9, 14, 15, 18-27]. The lack of definition about Pitcairnioideae positioning among subfamilies and their polyphiletic status resulted in the proposed division of the family into eight subfamilies: Brocchinioideae, Lindmanioideae, Hechtioideae, Navioideae, Puyoideae, Pitcairnioideae, Bromelioideae and Tillandsioideae [23, 24]. Nevertheless is important highlight three main aspects: (1) though the analyses had representatives of almost all genera of the family, only 90 species of a total of 3248 (*sensu* Luther [1]) were considered, and 12 genera have not yet been tested; (2) further assessments are required among species of Puyoideae that is considered monophyletic with low support using parsimony, and paraphyletic in the

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analyzes of Maximum Likelihood and Bayesian inference; (3) The hypotheses by Givnish *et al.* [23, 24] still need to be tested using nuclear genome and morphological data, since it is based only on data from the plastid genome.

Although this unstable scenario the monophyly of Tillandsioideae is well-supported, even by morphological, as well as molecular studies [6, 18, 20, 22-24, 27-29]. In comparison with the phylogenetic analyzes for the family, relationships within Tillandsioideae were investigated with broader taxon sampling, since included representatives of all genera [6, 29]. However, as example of the analyses performed for the family, those focused in Tillandsioideae the number of taxa sampled is still limited to a maximum percentage representing 9.4% of the species (*e.g.* [29]). Further more, as in other Bromeliaceae, phylogenetic studies in Tillandsioideae require testing using data from the nuclear genome and also morphological data. In the current classification Tillandsioideae is composed by four tribes: Catopsideae, Glomeropitcairnieae, Vrieseeae and Tillandsieae [29], including ten genera with approximately 1300 species: *Alcantarea* (E. Morren ex Mez) Harms (28 spp.), *Catopsis* Griseb. (18 spp.), *Glomeropitcairnia* (Mez) Mez (2 spp.), *Guzmania* R. & Pav. (210 spp.), *Mezobromelia* L. B. Sm. (9 spp.), *Racinaea* M. A. Spencer & L. B. Smith (65 spp.), *Tillandsia* L. (620 spp.), *Viridantha* Espejo-Serna (6 spp.), *Vriesea* Lindl. (266 spp.) and *Werauhia* J. R. Grant (87 spp.) (*cf.* [1, 25]).

The generic delimitation in Tillandsioideae has been widely discussed over the past seven decades, due seminal taxonomic studies of Baker [30], Mez [31] and the indispensable revision of Smith & Downs [8]. All these contributions are based mainly on dried specimens from herbaria that in many cases are not well preserved, leading to difficulties for a detailed floral analysis. It can be added to the fact that often important floral parts are absent [20], imposing a major difficulty in the selection of diagnostic characters for the taxa, resulting in an inaccurate circumscription of many genera. Consequently, changes in generic level are frequent, only highlighting some of the newest treatments such as several species of *Guzmania* transferred to *Mezobromelia* [32]; *Racinaea* was erected from *Tillandsia* subg. *Pseudo-Catopsis* [33]; many species of *Vriesea* were transferred to *Tillandsia* [34-36]; the generic status of *Alcantarea* was reestablished [37, 38], and finally two new genera were proposed, *Werauhia* [35, 37] from Central and northern South America, and *Viridantha* [39] the newest genus of the subfamily from Mexico. In despite of numerous transfers and changes generic in Tillandsioideae there is not yet a study bringing together its systematic history. Based on the information discussed above, the aim of this paper is to provide an update phylogenetic and history for the genera of Tillandsioideae.

RESULTS

Brief History of Taxonomy of Genera Tillandsioideae

Tillandsia, type of the subfamily was described by Linnaeus [40] in "Species Plantarum…". It is distinguished from other genera by inflorescence with one or more spikes with distichous arrangement (distichous flower arrangement), or rarely reduced to a spike with polystichous arrangement, or even isolated flowers [8]. Traditionally subdivided into nine [31], seven [8], or six subgenera essentially distinguished by characteristics of the inflorescence, sepals, petals and stamens: *T.* subg. *Allardtia* (A. Dietr.) Baker, *T.* subg. *Anoplophytum* (Beer) Baker, *T.* subg. *Diaphoranthema* (Beer) Baker, *T.* subg. *Phytarrhiza* (Vis.) Baker, *T.* subg. *Pseudoalcantarea* Mez, and *T.* subg. *Tillandsia*. This marked subdivisions supported by different authors [8, 31, 41] demonstrates that the genus possibly present distinct lineages. Five of the seven subgenera were reviewed: *T.* subg. *Tillandsia* [42, 43], *T.* subg. *Diaphoranthema* [44], *T.* subg. *Pseudo-Catopsis* segregated for *Racinaea* by Spencer & Smith [33] and *T.* subg. *Pseudoalcantarea* [45], and *T.* subg. *Anoplophytum* [46]. Gardner [43] studied the floral characters of various species of *T.* subg. *Tillandsia* and circumscribed five taxonomic groups. The stamens were considered rich in morphological features and the disposal of anthers and filaments the basis used of characters for the proposed taxonomic groups. Although preliminary, this study suggested more infrageneric subdivision pointing distinct morphological groups in the subgenus. Tardivo [46] in the taxonomic revision of the *T.* subg. *Anoplophytum* pointed out that this subgenus (*sensu* [8]) is monophyletic based on the presence of stigma simple-erect and plicate filaments, with exception of a basal group of species in the subgenus, which lacking plicated filaments. It is noteworthy that *T.* subg. *Allardtia* and *T.* subg. *Tillandsia* sharing plicate filaments [47], being this feature homoplastic, if considering the monophyly of the subgenera. Despite of these studies, the circumscription of subgenera in *Tillandsia* deserves to be discussed. In the current sense, *Tillandsia* is the largest genus of the subfamily and for entire

Bromeliaceae [1]. The status para or polyphyletic of genus and its subgenera has been demonstrated in analyzes based on molecular data [6, 20, 22, 29], demonstrating be required additional phylogenetic studies and revisional for stable and comprehensive hypotheses.

The genus ***Guzmania*** was described by Ruiz & Pav. [48] stands out morphologically from other Tillandsioideae by having sepals ecarinate and connate (rarely free) for more than half of petal length, and spikes with flowers always polystichous arranged, petals naked and agglutinated in a tube [8]. The complex species of *G.* subg. *Sodiroa* André and *G.* subg. *Massangea* E. Morren which have already been considered as distinct genera from *Guzmania*, distinguished from other species in the genus by presence of highly connate sepals for more than half its length in a cylindrical tube [8]. Betancur & Miranda-Esquivel [49] based on phylogenetic analysis, considered *Sodiroa* as a group potentially natural, and suggested to be elevated to generic category, while *Massangea* as paraphyletic. However, Betancur & Miranda-Esquivel [49] propositions was not widely accepted, not even corroborated by subsequent studies [29], and the genus *Guzmania* is current accepted in a single group (*sensu* [1]). However in molecular analyzes is controversially considered paraphyletic [29] or monophyletic [24]. Third largest genus in number of species of Tillandsioideae (ca. 210 spp.), it is yet little sampled in phylogenetic analyzes with no more than 14 species till now. Thus, analyses including a larger number of terminals of *Guzmania*, and a careful revision are required to understand their phylogenetic relationships.

The first author to describe species that would later be known as ***Vriesea*** was Hooker [50]. Later, Lindley [51] described the genus *Vriesea* to accommodate a single species *Tillandsia psittacina* W. J. Hooker, from the state of Rio de Janeiro, Brazil, using basically the presence of appendages at the base of the petals (ligules *sensu* Lindley [51]), in distinction the absence of such structures in *Tillandsia*. Several authors studied the taxonomy of the genus, numerous new species has been published, transferring species, adding and deleting of infrageneric categories of which Beer [52], Grisebach [53], Wawra [54, 55], Koch [56], Mez [57, 58], Smith [59] and Smith & Downs [8] must be highlighted. In the current sense the sections *Vriesea* and *Xiphion* are still used, although known as artificial by recent phylogenetic analyses [25, 26]. The taxonomic discussion of genus in recent decades rounded to emphasis of the adoption the presence of petal appendages as distinction between *Vriesea* and *Tillandsia* [8, 31, 60]. This feature has been the subject of incisive critics (*e.g.* [59, 61-63]). *Vriesea* is the second largest genus with ca. 270 species [1, 25], at present according to phylogenetic analysis is a polyphyletic assemblage of species [6, 18, 25, 29]. But these analyzes were based on comparatively small number of sampled taxa. An analysis with broad taxon sampling was undertaken to define the identity of *Vriesea s.s.* (the lineage of the type species *T. psittacina*) with a taxonomic overview of the genus and will be published in elsewhere [64].

The German botanist A. H. R. Grisebach [53] was the first author to publish a complete diagnosis for ***Catopsis*** Griseb. which is recognized as a distinct group by subsequent authors (*e.g.* [8, 30, 31, 58, 65]). Its diagnostic features are sepals strongly asymmetric for most species and seeds with apical appendage developed [8] and non-homologous to other genera in Tillandsioideae [66, 67]. Currently has about 18 species [1], considered monophyletic, basal in the subfamily, and clearly distinct from the *Vriesea*-*Tillandsia* clade [19, 20, 23, 24, 27] and one of the only distinct genera and without difficulties in circumscription among all Tillandsioideae.

The enigmatic ***Glomeropitcairnia*** (Mez) Mez, smallest genus in the subfamily, with only two species: *Glomeropitcairnia penduliflora* (Grisebach) Mez first described as *Tillandsia penduliflora* Grisebach [53] and *Glomeropitcairnia erectiflora* Mez. These species were initially placed in Pitcairnioideae by Mez [58] because the half-inferior ovary, partially indehiscent capsule and seeds with apical and basal appendage versus the superior ovary, capsule dehiscence and seed with appendage basal characteristic of the subfamily. Subsequently, Baker [30], Harms [38] and Mez [31] positioned the genus in Tillandsioideae, however, the last two studies considered the genus belonging to tribe Glomeropitcairneae. Smith & Downs [8] maintained the genus within Tillandsioideae but abandoning the tribe. For possessing morphological features typical of subfamily, some studies were demanded to evaluate the placement of the genus [6, 68]. At the moment, *Glomeropitcairnia* is clearly defined and its inclusion among Tillandsioideae genera corroborated by several studies [6, 20, 24, 68]. Although *Glomeropitcairnia* exhibit two distinct features in the subfamily (*i.e.* half-inferior ovary, interpreted as autapomorphy, and seed with apical and basal appendages well developed), its species presenting

floral features and leaf morphology of Tillandsioideae [6, 69], and stigma type have convolute-blade [70].

First treated as a subgenus of *Vriesea,* ***Alcantarea*** (E. Morren ex Mez) Harms [57], was first elevated to generic status by Harms [38]. However Mez [31] reestablished *Alcantarea* to the category of subgenus of *Vriesea*. Smith [71, 72] and Smith & Downs [8] maintained the status proposed by Mez. Only sixty-one years after Grant [37] reclassified *Alcantarea* restoring its generic category, supported by the distribution restricted southeastearn and northeastearn Brazil additional to the floral characters petals long and linear, flaccid and ephemeral and seed with basal and apical coma developed. The genus was recently revised [73] and important features were reevaluated, in a study highlighting significant changes in the interpretation of morphology of Tillandsioideae. According Versieux [73] *Alcantarea* possess cryptically half-inferior ovary with hypanthium, in opposition to the superior ovary suggested by other studies [8, 28], the half-inferior ovary was pointed as a feature of *Glomeropitcairnia* exclusive. This information necessarily brought changes to the optimization of this precedent synapomorphies of the subfamily. In the current sense *Alcantarea* is monophyletic [26] and distinguished by having only rupicolous habit, petals long, linear and ephemeral, cryptically ovary half-inferior ovary with hypanthium, obovate petal appendage, and seeds with coma at the base and apex [73].

Mezobromelia L. B. Sm. is the second smallest genus of the subfamily, with only nine species distinguished by having always polystichous inflorescences, rare distichous, short sepals connate or connate petals firmly agglutinated and stamens connate [8] and epipetalous [32]. *Mezobromelia* together with *Guzmania*, presents polystichous arrangement in the most species, and species belonging to *Mezobromelia* are distinguished from *Guzmania* by presence of petal appendage absent in *Guzmania*. Phylogenetic analyzes not support the monophyly of the genus, its poliphyly has been recurrently demonstrated [24, 29].

Based on a reevaluation of *Tillandsia* subg. *Pseudo-Catopsis*, Spencer & Smith [33] pointed out distinct features considered by them as sufficient for the establishment of the new genus ***Racinaea.*** The set of diagnostic characters to distinguish from other Tillandsioideae flowers are inconspicuous, small and distichous, asymmetrical sepals and stamens and pistils included in the corolla. *Racinaea* species have so far been poorly sampled in phylogenetic studies, despite the small number of species assessment, its monophyly is questioned, being demonstrated to be paraphyletic [20], or monophyletic [29].

The history of the genus ***Werauhia*** started with 38 species transferred from *Thecophyllum* (*sensu* Mez [31]) to *Vriesea* by Smith & Pittendrigh [74]. This small group of species assigned to the genus *Vriesea* sect. *Xiphion* (*sensu* [8]) named as "Thecophylloid *Vrieseas*" with distribution restricted to Central America, of which 80% occurs only in Costa Rica and western Panama was reviewed by Utley [75]. Characterized by inflorescences compound, secondary reduced or aborted, short branches and subtended by well-developed primary bracts [75], corolla zygomorphic, dactyloid petal appendage, and stigma cupulate without papillae [37]. Later, Grant [37] distinguished the similarity and homogeneity of the group already shown by Utley [75], erected the genus *Werauhia*. The description of a new genus was necessary because the type species of *Thecophyllum* sensu André [76] belongs to *Guzmania*. The current genus *Werauhia* includes both species with compound and simple inflorescence (*e.g. Werauhia gladioliflora* (H. Wendland) J. R. Grant and *Werauhia viridiflora* (Regel) J. R. Grant) with species occurring in Central America, Caribbean, Andean, Amazonian and Guiana Highlands. The monophyly of the lineage of *Werauhia* (*e.g*. [29]), supports its generic establishment.

Viridantha is the most recent genus to be designated to subfamily it was erected to accommodate species previously classified in *Tillandsia* subg. *Tillandsia*, the *Tillandsia plumose*-complex of Baker [30]. The genus is endemic to Mexico, and is characterized by presenting homodynamous stamens (subequal stamens), filaments flattened, distichous flowers, stigma simple-erect. Corroborating this circumscription it was identified as monophyletic [29].

DISCUSSION

Tillandsioideae is striking by its richness having the highest number of bromeliads species, of which are distributed in fewer genera than all other subfamilies [1], depicting a high morphological diversity (Figure **1**) and also a major challenge for taxonomists. Considering that taxonomic endeavor in Tillandsioideae involves more than 1300 it is understandable that many uncertainties still remain. However, significant progress has been made, especially in the past decade mainly in

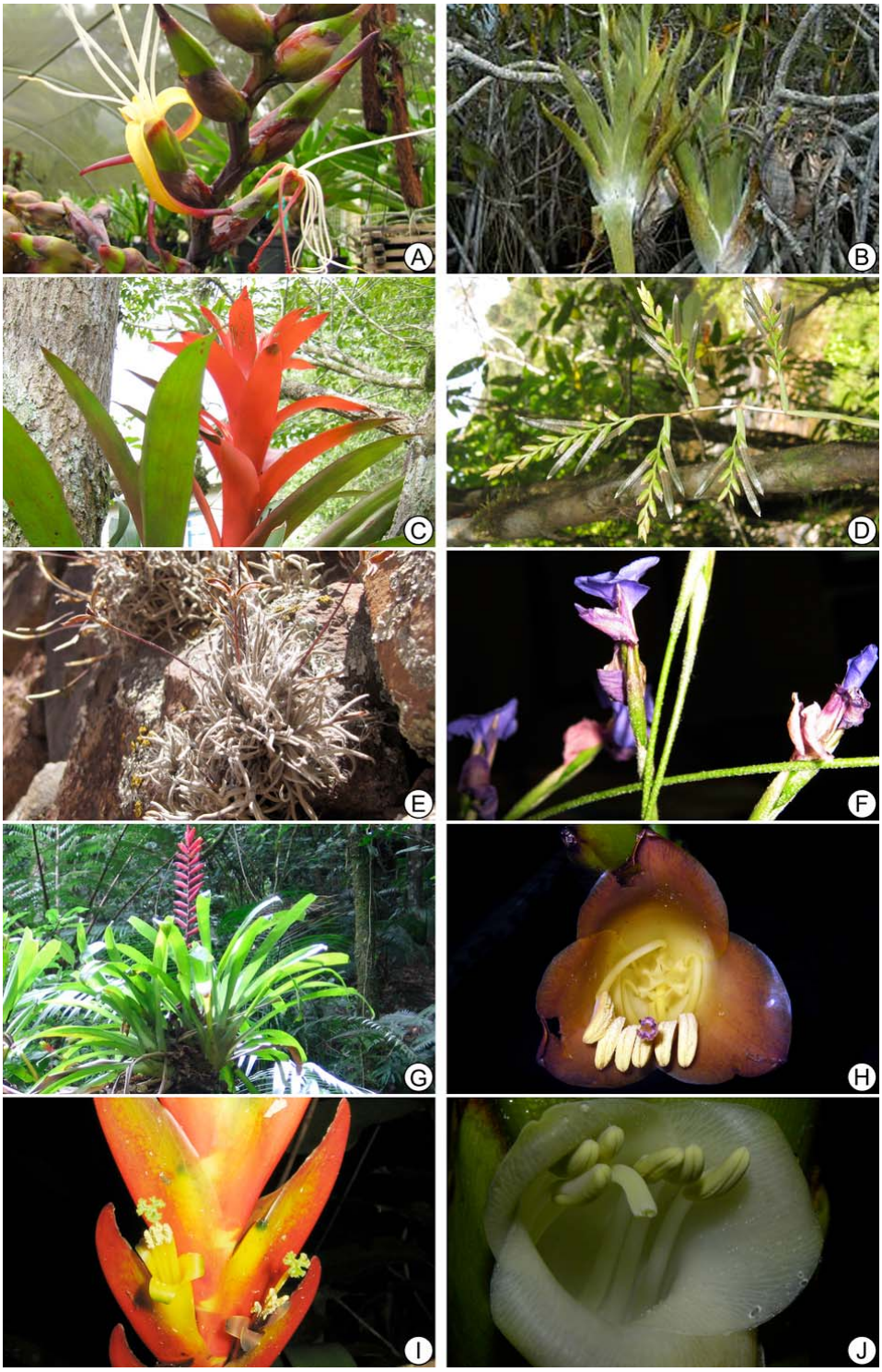

Figure 1: (A-J). Vegetative and floral diversity of some species of Tillandsioideae. **A.** *Alcantarea vinicolor* (E. Pereira & Reitz) J.R. Grant, details of the flower with long petals and linear; **B.** *Catopsis berteroniana* (Schultes f.) Mez with leaves covered by white coat waxes conspicuous; **C.** *Guzmania lingulata* (Linnaeus) Mez, spikes with flowers always polystichous arranged; **D.** *Racinaea spiculosa* (Grisebach) M.A. Spencer & L.B. Smith, flowers are inconspicuous, small and distichous; **E.** *Tillandsia recurvata* (Linnaeus) Linnaeus, with stem typically much shorter than the leaves; **F.** *Tillandsia mallemontii* Glaziou ex Mez, with petal blue or violet of rare occurrence in other genera of Tillandsioideae; **G**. *Vriesea gradata* (Baker) Mez, flowers distichous arranged typical of the genus; **H.** *Vriesea bituminosa* Wawra, included stamens in section *Xiphion*; **I.** *Vriesea incurvata* Gaudichaud, exserted stamens in section *Vriesea*; **J.** *Werauhia gladioliflora* (H. Wendland) J.R. Grant, stigma cupulate without papillae. (Photos by Gomes-da-Silva, J.; Moura, R. and Pinto, A.)

phylogenetic relationships (*e.g.* [25, 26, 29]), and reviews of small groups of species (*e.g.* [77-79]). Despite the large number of studies and researchers focused on Bromeliaceae, it is imperative that many data are still explored, accumulated and assembled into a phylogenetic hypothesis with greater accuracy, mainly in the genera *Vriesea* and *Tillandsia* they are undoubtedly the greatest richest and with higher taxonomic difficulties and both has been acknowledged as polyphyletic genus, plus *Mezobromelia* which has been demonstrated as an unnatural group.

ACKNOWLEDGEMENTS

The authors express their thanks to Coordenação de Aperfeiçoamento de Pessoal de Nivel Superior - CAPES for the fellowship to the first author from PROTAX program, and Conselho Nacional de Desenvolvimento Científico e Tecnológico - CNPq for the grant in research productivity to the second author. This research was part of Doctor thesis by the first author at Programa de Pós-Graduação em Ciências Biológicas Botânica - Universidade Federal do Rio de Janeiro.

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Received on 18-10-2013 Accepted on 31-12-2013 Published on 18-02-2014