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The Morphological Variation of the Genus *Rhododendron* (Ericaceae) in Himalayan Ranges of Bhutan

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ABSTRACT.– Bhutan Himalayan ranges harbor 46 species of *Rhododendron* and contributes four percent of the genus in the world. The genus *Rhododendron* is associated with morphologically diverse, complex vegetative and floral traits. The variation of floral traits of rhododendrons might have attributed due to the pollinators and adaptive preference resulting in the evolution of floral complexity. However, there is a paucity of scientific studies concerning the vegetative and reproductive morphology of rhododendrons and pollinators. A comparative morphological study was investigated on 30 species of *Rhododendron* from different geographical locations of Bhutan. We studied the interspecific variation of seed and pollen morphology among the selected species. Casual pollinator observations were also examined to identify the potential pollinators and visitors through in-person and binocular. Eight different floral types and two seed types were identified from the present study. We suggest that the floral morphology and distribution of *Rhododendron* floral types over the landscape may reflect their adaptive value of the plant-pollinator interactions. Additionally, seed traits might have influenced the dispersal ability and colonization of species. Further in-depth explorations on floral development, pollination ecology, and seed developmental allometry may offer a broader understanding of the floral evolution, specialization in plant-pollinator interaction in angiosperm, and their adaptation to the unique environmental cline of the Himalayas.

KEY WORDS: morphology, pollination syndrome, *Rhododendron*

INTRODUCTION

The genus *Rhododendron* L. belongs to the family Ericaceae, which is found in cool broadleaf forests to the alpine zone exhibiting an extraordinary floral diversity (Davidian, 1989; Chamberlain et al., 1996, Cullen, 2005). The word "*Rhododendron"* came from the Greek words: "rodon" which means "rose" and "dendron" meaning "tree" hence a rose tree. It is one of the largest and most diverse genera of the family Ericaceae that is composed of ca. 1,000 species. The genus is categorized into eight subgenera namely, Subgenus *Hymenanthes* (elepidote rhododendrons, 302 species), Subgenus *Tsutsusi* (evergreen azaleas, 117 species), Subgenus *Pentanthera* (deciduous azaleas, 30 species), Subgenus *Therorhodion* (1 species), Subgenus *Azaleastrum* (10 species), Subgenus *Candidastrum* (1 species), Subgenus *Mumeazalea* (1 species), and Subgenus *Rhododendron* (lepidote Rhododendrons, 542 species) (Chamberlain et al., 1996, Cullen, 2005). It is mostly found in the northern hemisphere, especially in Asia, Europe, and North America (Georgian et al., 2015) distributed within the range of 65º north to 20º south latitude in tropical, temperate, and boreal zones (Wang et al., 2014). In particular, a majority of the genus *Rhododendron* population is found in eastern Himalayan ranges, which include Bhutan, Nepal, Sikkim, eastern Tibet, Arunachal Pradesh, northern Myanmar, and western and central China (Cullen, 2005). The subgenus *Rhododendron* Section *Vireya*, is found in the Malesian region through the Indo-Australian archipelago (Yoichi et al., 2019).

Rhododendron is the only plant taxon that grows on a continuum ecotone from the lower montane forest to alpine zone in the Himalayas (Huang et al., 2017, Singh et al., 2009). Its topographic complexity and diverse habitat offer the most extended bioclimatic conditions for the plant to grow with different floral morphological and physiological traits (Grytnes and Vetaas, 2002). However, the floral variation among the species and the potential pollinators associated, that may have caused the alteration of morphological traits of angiosperm have received much consideration in the field of ecology (Scaven and Rafferty, 2013).

So far, 46 species of the genus *Rhododendron* (Long, 1991, Pradhan, 1999) within two subgenera, i.e., *Rhododendron* and *Hymenanthes* are recorded in the Himalayas of Bhutan. Altitudinally, it grows from 2500-4700 m above sea level (asl) and it is found in almost all mountain habitats (Jamtsho and Sridith, 2015) contributing around four percent of the species in this genus (Namgay and Sridith, 2020). However, little information of interest exists in the study of morphological variation of *Rhododendron* in the Himalayan region, particularly in Bhutan. Moreover, the plant-pollinator interactions (pollination syndrome) of *Rhododendron* species of Bhutan are least studied and the concept of pollination syndrome is mostly viewed as a generalized one.

The morphological study of rhododendrons over the heterogeneous landscape coupled with the uneven distribution of pollinator faunas may provide insightful information on understanding their mechanism of adaptability and coevolution between flower and the pollinators (Galen and Cuba, 2001). Additionally, morphological study of alpine and upper mountain plant species such as *Rhododendron* could provide baseline information on the plant-pollinator interaction in the wake of climate change. Therefore, the present study was conducted to examine the morphological variations of the genus *Rhododendron* and explore how the taxa within the genus are distributed throughout the Himalayan ranges of Bhutan.

We hypothesized that *Rhododendron* species would exhibit a significant vegetative and floral morphological trait due to its wide distributional range along the elevation gradient with different environmental regimes. Additionally, the difference in physiological adaptation and differential pollinators service may contribute to the evolution of diverse floral and vegetative morphological traits. This paper attempt to explain the detailed account of the morphological variation of the genus and the speculative part concerning pollination ecology. We hope that it will inspire and generate more interest in this genus through a scientific approach and collection of more data from the field. In this paper, we specifically addressed the following research question: (a) What is the morphological variation of genus *Rhododendron* in Bhutan Himalayan ranges? It is important to answer this question to understand how plant traits are adapted and interact with the pollinators in the extreme and unique environments in the Himalayas.

MATERIALS AND METHODS

Study sites

A survey was conducted in seven geographical locations of Bhutan i.e., Chelela (27°37.31′N; 89°37.27′E), Dochula (27°48.34′N; 27°48.34′E), Pelela (27°51.70′N; 90°54.89′E), Yotongla (27°52.14′N; 90°60.93′E), Phrumsengla National Park (27°39.84′N; 90°99.41′E), Dagala (27°26.58′N; 89°65.26′E) and Sakteng wildlife sanctuary (27°41.85′N; 91°87.62′E) (Fig.1).

Specimen collections

The study was conducted during the flowering and fruiting season between March and September 2019 at regular intervals.

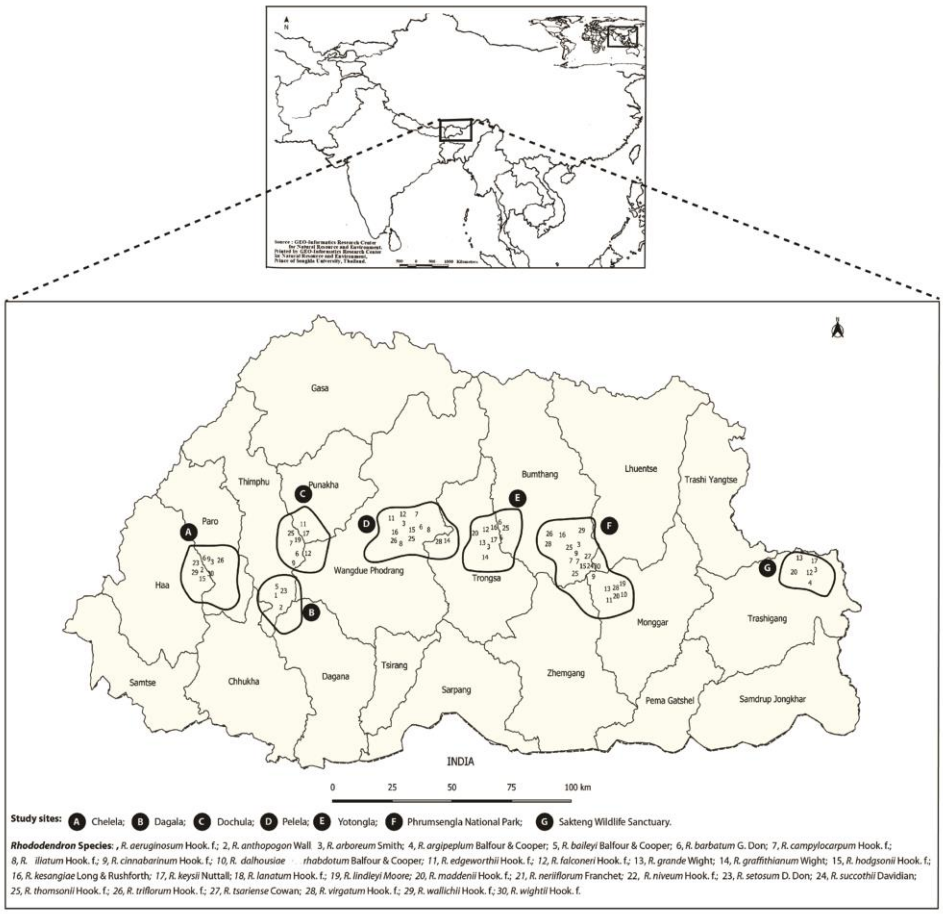

FIGURE 1. Map showing the study sites of the different geographical locations of the Himalayan ranges of Bhutan

Thirty species of *Rhododendron* were studied from different geographical locations of the Himalayan ranges of Bhutan. Furthermore, detailed morphological traits were also studied. From October till December 2019, we collected the matured fruits and dried them at room temperature until further use. When the fruit capsule was thoroughly dried, the seed was studied under a microscope (Olympus SZH10). Pollen morphology of selected *Rhododendron* species was studied using scanning electron microscopy (SEM) and light microscopy (LM). The scientific names of *Rhododendron* species in the present study were following Long, 1991. The voucher specimen was prepared using standard herbarium methods and deposited in the National Herbarium Centre, Serbithang, Thimphu, Bhutan.

Pollination observation

Casual pollinator censuses were observed for at least five hours during calm and clear days from 7.00 am to 11.00 am. The pollinators that are within the range of vision were photographed for identification. The visiting species that are within the radius of 50 m were observed using the binocular. Those birds and insects which dipped their head into the corolla tube touching anther and stigma were recorded. The pollinators were photographed

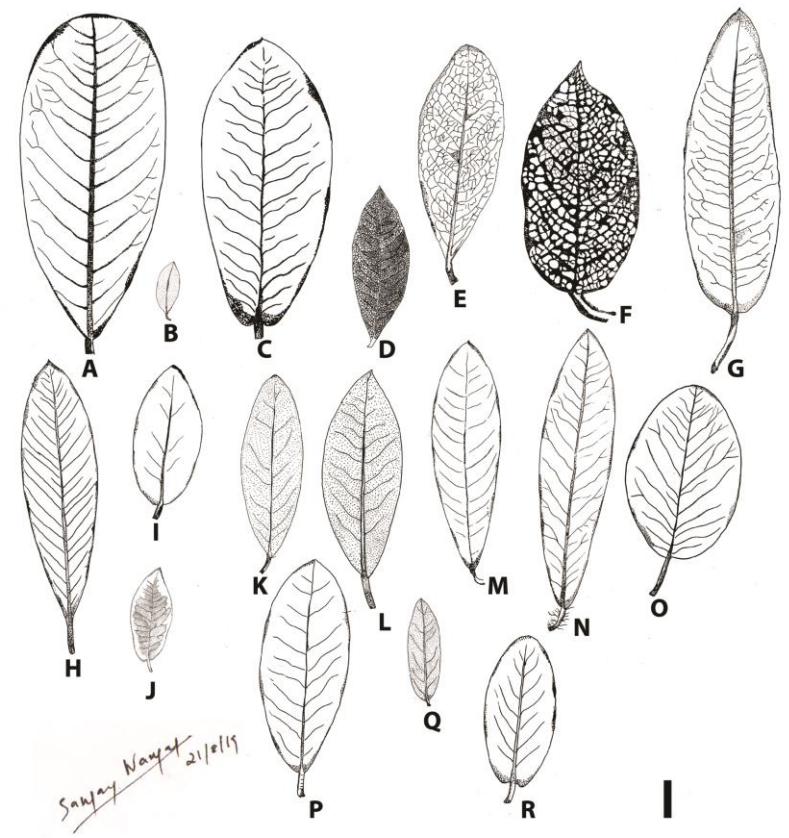

FIGURE 2. Leaves of selected *Rhododendron* taxa. (Scale bar 1 cm; all the same magnification) **A,** *R. kesangiae*; **B,** *R. baileyi*; **C,** *R. barbatum*; **D,** *R. ciliatum*; **E,** *R. dalhousiae* var. *rhabdotum*; **F,** *R. edgeworthii*; **G,** *R. graffithianum*; **H,** *R. grande*; **I,** *R. lanatum*; **J,** *R. triflorum*; **K,** *R. lindleyi*; **L,** *R. maddenii*; **M,** *R. niveum*; **N,** *R. succothii*; **O,** *R. thomsonii*; **P,** *R. wightii*; **Q,** *R. virgatum*; **R,** *R. wallichii*

and identified from the *Birds in Bhutan* (Spierenburg 2005) and bees and insects were identified in consultation with entomologists.

RESULTS

The morphological characteristics.

I. Vegetative character

Growth forms

Different growth forms can be observed among *Rhododendron* species. It ranges from creeping scrub, i.e., *R. setosum* and *R. anthopogon* (Plate 1, D) to a tree, e.g., *R. arboreum* and *R. kesangiae* (Plate 1, A). Above treeline, *Rhododendron* "krummholz" such as *R. aeruginosum* (Plate 1, C) is found in deformed vegetation with stunted growth due to continual exposure to fierce environmental factors such as freezing winds and frequent snow cover. Rhododendrons of prostrate scrub and krummholz is the only plant taxa found above the treeline of the same altitude all over the Himalayan ranges of Bhutan.

Leaves

The leaves are mostly oblanceolate in shape, and the sizes of the leaves vary from few millimeters, e.g., *R. baileyi* (Fig. 2, B) to almost half a meter, e.g., *R. falconeri* (Table 1). Generally, the leaves of *Rhododendron* are

TABLE 1. Seed variation of *Rhododendron* species

Seed Type	Seed morphological description	Example
Type 1	Seeds slightly flattened or elongated; well-developed basal, apical, and lateral wings. Deeply dissected either from the basal or apical wing, Lateral wings usually broad 120 µm.	*R. maddenii*
Type 2	Small and elongated; outline elliptic and gradually tapering at both the end. Minute lateral wings.	*R. setosum*

coriaceous with scales, e.g., *R. maddenii* and some with indumentum forming a thick hairy-like structure below the leaf surface as in *R. edgeworthii*. Some exceptions like *R. neriiflorum*, where both sides of the surfaces remain glabrous. Almost in all tree rhododendrons, the leaf is to some extent arranged in spiral forming false whorls with very short internodes at the terminal branches. However, those shrubby species of epiphytic, rocky edges and on the marshland are arranged alternatively.

II. Reproductive characteristics

Inflorescences

The inflorescence in most *Rhododendron* species is umbellate raceme where the flowers are borne from a stalk of almost to the same point of axis with a short pedicel as found in *R. arboreum*, *R. hodgsonii*, and *R. kesangiae*, etc. However, a loose raceme with a long pedicel is seen in a few species, such as *R. dalhousiae* var. *rhabdotum* and, *R. graffithianum*, etc.

Calyx

The shape and size of the calyces differ considerably among the species, and most of the calyces are often reduced and inconspicuous. In some plants, calyces are well-developed with distinct calyx lobes. Some species have round short-lobed calyx of ca. 6.1 ± 8.7 mm long, glabrous, and spreading, e.g., *R. graffithianum* (Fig. 3, A1). In some selected taxon, short-lobed calyx forming cup shape could also be seen, i.e., *R. thomsonii* (Fig. 3, F2), or in other taxa, the calyx is deep-lobed with hairy like structure such as in the case of *R. ciliatum.*

Corolla

Most *Rhododendron* species are associated with a long or short basal tubular part of sympetalous with varying degrees of lobes. Corolla lobe of some species is reflexed, e.g., *R. griffithianum* and *R. lindleyi* (Fig. 3, A1; A2). Some taxa of *Rhododendron*, e.g., *R. setosum* (Fig. 3, H1), has a spreading corolla lobe that is longer than the corolla tube; therefore, it looks "polypetalous like". In the case of *R. baileyi* (Fig. 3, D; Plate 2, d), the corolla lobe is ± perpendicular to the corolla tube while the corolla lobe of *R. keysii* is rather short and erect (Fig. 3, C; Plate 2, c), therefore looks "lobeless" like. However, in many *Rhododendron* species, the corolla lobes are suberect. The corolla is glabrous outside, however, very few exceptions like *R. ciliatum* where indumentum could be detected at the base of the corolla tube, and the corolla tube of *R. anthopogon* is tomentose inside. The corolla tube may be ± straight to ± curve in most species, e.g., *R. keysii* and the tube length varies considerably from rather long as in *R. dalhousiae* var. *rhabdotum* to a short one in *R. setosum*, etc.

Androecium

Usually, *Rhododendron* has 10 stamens with unequal lengths, which is arranged around the ovary. In any case, the number of stamens could vary between 10-15. Each stamen has a long filament with a tuft of hair towards the base. The anthers are open through apical pores only.

Gynoecium

The ovary is *superior* cylindric-conical in shape with five locules. In most cases, the ovary is pubescent or scaly and rarely

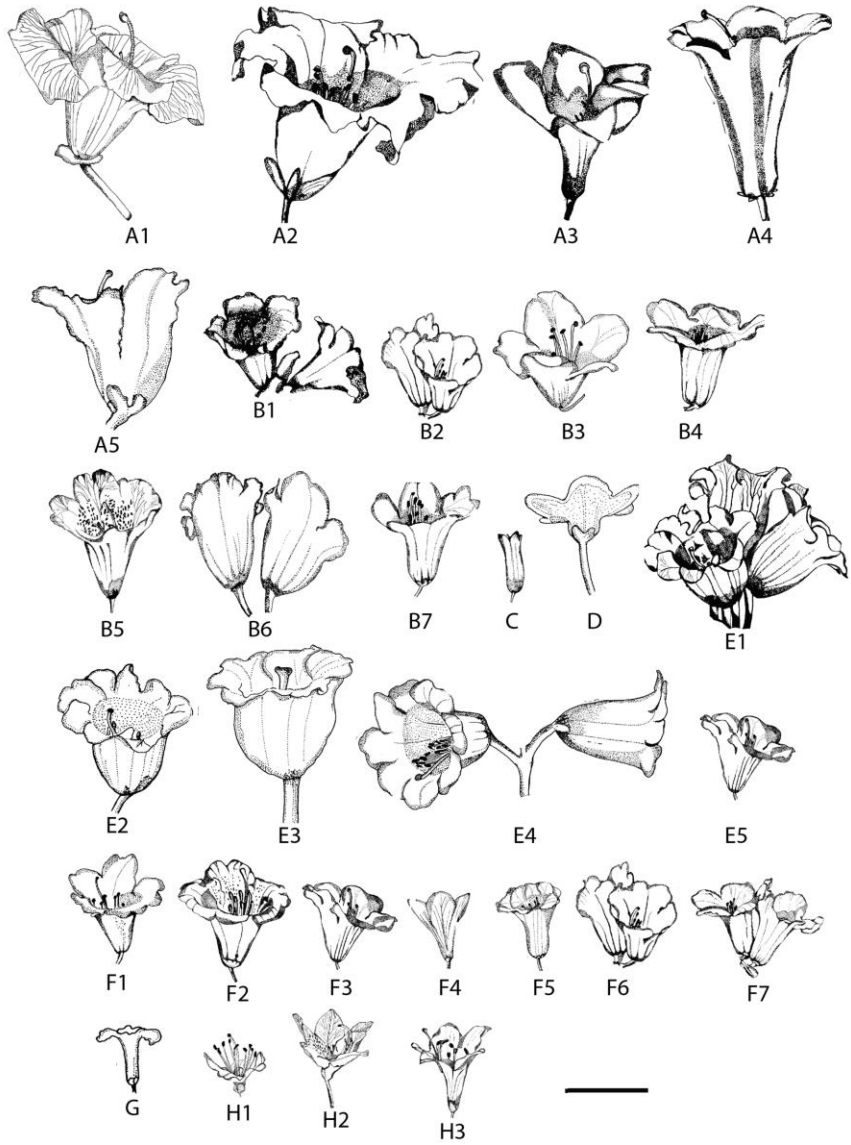

FIGURE 3. Floral morphology of *Rhododendron* in Bhutan Himalayan ranges. (scale bar 1 cm; all the same magnification) **Type A**: **A1,** *R. griffithianum*; **A2,** *R. lindleyi*; **A3,** *R. maddenii*; **A4** *R. dalhousiae* var. *rhabdotum*; **A5,** *R. edgeworthii.* **Type B**: **B1,** *R. lanatum*; **B2,** *R. ciliatum*; **B3,** *R. campylocarpum*; **B4,** *R. wallichii*; **B5,** *R. tsariense*; **B6,** *R. aeruginosum*; **B7,** *R. wightii.* **Type C**, *R. keysii.* **Type D**, *R. baileyi.* **Type E**: **E1,** *R. kesangiae*; **E2,** *R. hogsonii*; **E3,** *R. falconeri*; **E4,** *R. grande*; **E5,** *R. niveum.* **Type F**: **F1,** *R. argipeplum*; **F2,** *R. thomsonii*; **F3,** *R. barbatum*; **F4,** *R. cinnabarinum*; **F5,** *R. neriiflorum*; **F6,** *R. arboreum*; **F7,** *R. succothii.* **Type G**, *R. anthopogon.* **Type H**: **H1,** *R. setosum*; **H2,** *R. triflorum*; **H3,** *R. virgatum*

glabrous in selected taxa. The style length ranges from ca. 1.7 mm in *R. setosum* to 11 mm long as in *R. falconeri.* Concerning stigma, it is recurved and exserted in most cases, with few exceptions of the taxa that the stigma remains included, e.g., *R. baileyi* and *R. anthopogon*, etc.

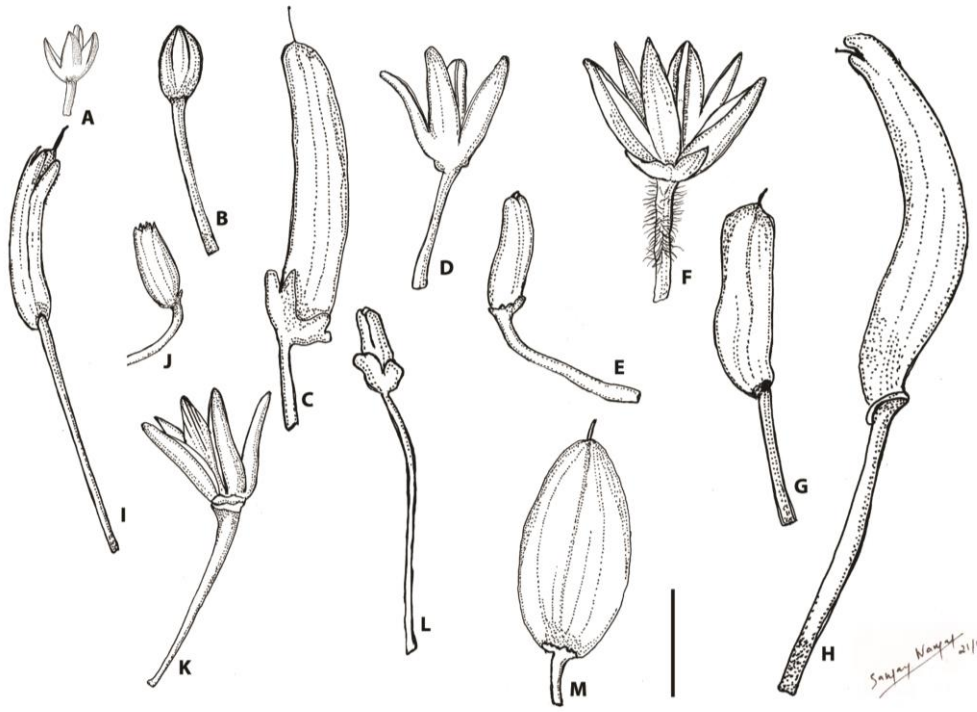

FIGURE 4. Fruits of selected *Rhododendron* species. (Scale bar 1 cm; all the same magnification) **A,** *R. anthopogon*; **B,** *R. baileyi*; **C,** *R. barbatum*; **D,** *R. campylocarpum*; **E,** *R. cinnabarinum*; **F,** *R. ciliatum*; **G,** *R. lanatum*; **H,** *R. hodgsonii*; **I,** *R. thomsonii*; **J,** *R. keysii*; **K,** *R. triflorum*; **L,** *R. setosum*; **M,** *R. maddenii*

Fruits and seeds

The mature capsule is conical or cylindrical in all taxa. The capsule opens loculicidal (Fig. 4, F; K). The capsule in selected species is pubescent, e.g., *R. edgeworthii*, etc. and scaly, e.g., *R. thomsonii*. The seeds are small, mostly elliptic to fusiform and raised externally by hexagonal anticlinal and periclinal cells (Fig. 5) surrounded by the wing-like structure with entirely or incomplete dissected forms e.g., *R. falconeri* (Fig. 5, 1A). Other seeds are small of ca. 200 µm and do not have wings e.g., *R. anthopogon* (Fig. 5, 2D).

Pollen

The pollen of eight selected *Rhododendron* species has been studied, i.e., *R. aeruginosum, R. baileyi, R. barbatum, R. cinnabarinum, R. lindleyi, R. setosum, R. thomsonii,* and *R. wightii* from different altitudinal gradients. In all the species, the pollen grains are generally arranged in tetrahedral tetrads, heteropolar, bilaterally symmetric with tricolpate aperture. Pollen of all the species has gemmate ornamentation. The length of the polar axis ranges from 19.25 - 33.50 µm, and the length of the equatorial axis varies from 26.28 - 1.43 µm with exine thickness ranges of 9.0 - 1.48 µm (Table 2).

Ecology

Rhododendron is found in diverse habitats from lower cool broadleaf forests to the higher alpine region of Bhutan Himalayan ranges. At the lower altitude (2500-3000 m asl.), most species grow under the canopy of coniferous forest along with bamboo shrub, e.g., *R. barbatum, R. falconeri, R. kesangiae,* and *R. hodgsonii*. Within this elevation range,

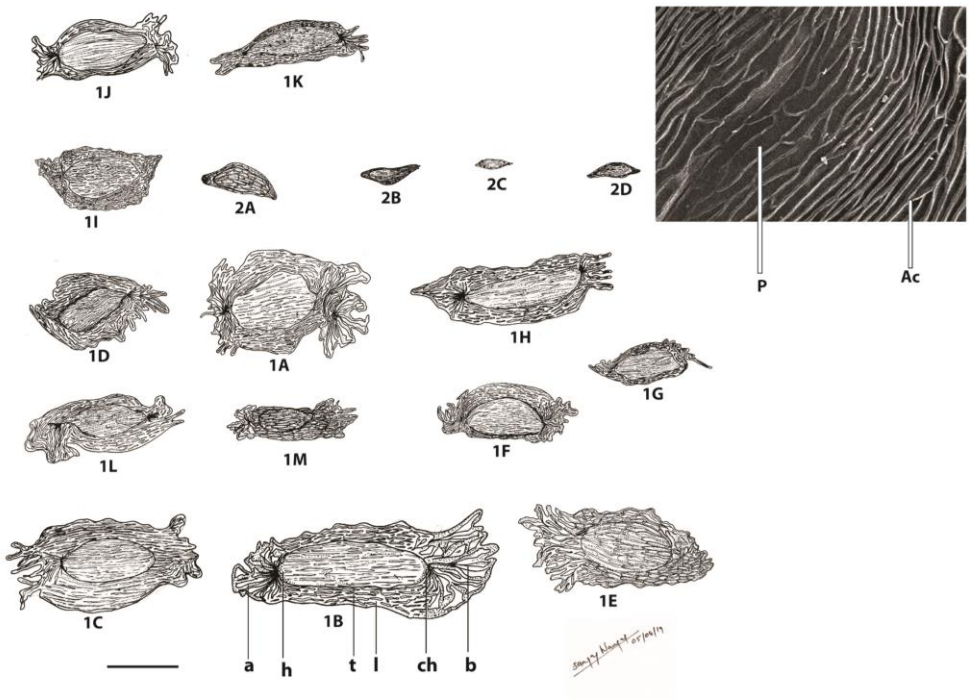

FIGURE 5. Diagram of seed variation in *Rhododendron*. (Scale bar 100 µm; all the same magnification) **Type 1**: **1A,** *R. falconeri*; **1B,** *R. grande*; **1C,** *R. dalhousiae* var. *rhabdotum*; **1D,** *R. kesangiae*; **1E,** *R. maddenii*; **1F,** *R. edgeworthii*; **1G,** *R. ciliatum*; **1H,** *R. griffithianum*; **1I,** *R. hogsonii*; **1J,** *R. wightii*; **1K,** *R. barbatum*; **1L,** *R. succothii*. **1M,** *R. arboreum*. **Type 2**: **2A,** *R. lanatum*; **2B,** *R. cinnabarinum*; **2C,** *R. setosum*; **2D,** *R. anthopogon* (**a**, apical wings; **h**, hilum; **t**, tegmen; **l**, lateral wing; **ch**, chalaza; **b**, basal wing; **P**, periclinal wall; **Ac**, anticlinal cell)

some species of *Rhododendron* are found under the cool broadleaf leave forest of lower montane mostly inhabiting a rocky cliff, e.g., *R. maddenii*, *R. edgeworthii*, *R. dalhousiae* var. *rabdotum*, *R. lindleyi*, and *R. griffithianum*. Other species such as *R. thomsonii* and *R. ciliatum* can be seen on disturbed mashland. It is interesting to note that *R. arboreum* is found in every habitat mentioned above. From 3000-3800 m asl, most of the species grows in the form of shrubby tree under the canopy of coniferous forest e.g., *R. succothii*, *R. lanatum*, *R. wallichii*, *R. wightii* and *R. cinnabarinum*, etc. Above timberline i.e., ca. 4000 m above, *Rhododendron* Krummholz e.g., *R. aeruginosum* and the creeping shrub of *Rhododendron* can be seen e.g., *R. anthopogon* and *R. setosum*.

DISCUSSION

This study was conducted to examine the variations of morphology in the genus *Rhododendron* in Bhutan Himalayas. Thirty *Rhododendron* species were evaluated during our study, and the genus exhibits a considerable floral diversity that grows naturally over the heterogeneous landscape of Bhutan Himalayan ranges. Eight floral types were recognized based on the flower shape, color, position of anther and stigma, and plausible pollinators. Additionally, two seed types were known based on the size and the wings. The result suggests that the difference in floral morphology might have occurred due to the pollinator selection pressure or behavior

TABLE 2. Floral types of *Rhododendron* with probable pollinators

Floral Type	Floral morphology	Species	Pollinators
Type A	It has a long parallel-sided tube with long corolla obtuse lobe; well-developed calyx with varying degree of lobes; exerted stigma and style; 10 stamens; wide opening diameter without nectar.	*R. graffithianum*; *R. lindleyi*; *R. maddenii*; *R. dalhousiae* var. *rhabdotum*; *R. edgeworthii*	Bees*
Type B	Ventricose-campanulate; presence of blotches on some species with different flower colors; reflexed, exerted stigma and stamens; 10 stamens; reduced calyx.	*R. lanatum*; *R. ciliatum*; *R. campylocarpum*; *R. wallichii*; *R. tsariense*; *R. aeruginosum*; *R. wightii*	Bees*
Type C	Narrow tubular with very short and erect corolla lobes; stigma and stamens are all arranged almost in the same plane. 10 stamens; actinomorphic corolla with reduced calyx	*R. keysii*	Birds*
Type D	Short corolla tube length with rounded base; long corolla lobes arranged slightly perpendicular from the axis; slightly zygomorphic; 10 stamens; short-included stigma and exerted stamens; well-developed calyx.	*R. baileyi*	Bees*
Type E	Obliquely campanulate with 8-9 short corolla lobes; exerted stigma; reduced calyx; slightly actinomorphic corolla; usually 12-15 bundle stamens of different length.	*R. kesangiae*; *R. hodgsonii*; *R. falconeri*; *R. grande*; *R. niveum.*	Birds*
Type F	Tubular-campanulate shaped flower with intermediate corolla tube length; short corolla lobes; monosymmetric corolla with 10 straight bundle stamens and slightly hooked flexion of styles. It is accompanied by nectar.	*R. argipeplum*; *R. thomsonii*; *R. barbatum*; *R. cinnabarinum*; *R. neriiflorum*; *R. arboreum*; *R. succothii*	Birds & Bees*
Type G	Narrow parallel-sided tube and widespread of corolla lobes; included stamens and stigma in the tube; 10 stamens; zygomorphic and well-developed calyx.	*R. anthopogon*	Bees & Insect*
Type H	Narrow funnel-shaped; short corolla tube length with long corolla lobe held ± horizontally; well-developed calyx; reflex or straight style; monosymmetric corolla; some species have blotches on one side of the corolla lobes.	*R. setosum*; *R. triflorum*; *R. virgatum*	Bees*

*= Pollinators through casual observation.

over long-term ecological time (Johnson 2010, Fenster et al., 2004). On the other hand, seed traits of *Rhododendron* might have evolved due to a trade-off between resource availability and seed production (Wang et al., 2014). It is realized that seed morphology determines the dispersal and strength of colonizing ability in a new or already established vegetation. However, further study is required to confirm the relationship between the floral type and the pollinators, since to our knowledge this is the first attempt of scientific study to examine the morphological variation of *Rhododendron* in Bhutan Himalayan ranges.

I. Variation in vegetative morphology

Habit

Rhododendron species are mostly woody plants that appear in different growth forms. It is the only plant taxon that is distributed from lower montane forest to alpine region on diverse habitats. At lower elevation 2500-3000 m asl, almost all the species grow under a dense mixed coniferous forest as a tree or shrubby tree form ranging from 15 to 20 m of height, e.g., *R. arboreum*, *R. kesangiae*, and *R. lanatum* etc. Here, we proposed that such tree form might have occurred due to the deprivation of light and competition for the mineral resources among trees as formerly proposed by Jamtsho and Sridith (2015). Many *Rhododendron* species are in "erect shrubby tree form," e.g., *R. ciliatum*; *R. thomsonii*, etc. (Plate 1, B). They are mostly found either in the disturbed areas with excess sunlight such as disturbed forests, wetlands and even on the abandoned agricultural land. Above treeline, it grows with unique life

forms, i.e., erect shrubs that are grouped in dense krummholz plant i.e., *R. aeruginosum* (Plate 1- C) and creeping shrub forming low cushion mats, i.e., *R. setosum* and *R. anthopogon* (Plate1, D). Such different growth forms in the alpine landscape might be attributed to the ecological constraints such as short growing season, high wind velocity, and low soil levels of mineral nutrients (Körner, 1998; Bharali et al., 2011; Jamtsho and Sridith 2015).

Leaves

There is a variation of shapes and sizes of leaves among the congeneric species of *Rhododendron*. The species that grow in forest vegetation have rather long tapering leaves mostly in either oblong or oblanceolate shape, and it is associated with loose indumentum and scales beneath the leaf. The young plants have a large surface of leaf than the tree ones. The thick canopy layer of conifer trees and adult plants may have caused photoinhibition to the under canopy plants such as rhododendrons which could be plausibly inferred that *Rhododendron* taxa occurring in this habitat has large leaf surface area which is arranged in a cluster at the end of the branches almost forming false whorls so that they can harvest solar energy for their growth e.g., *R. falconeri* and *R.kesangiae,* etc. While the ones that occur in open areas such as a bog or alpine meadow, and wetlands have smaller leaves with mostly elliptic shape with an alternate arrangement. Some species occurring in the rocky cliff have dense indumentum e.g., *R. edgeworthii* (Fig. 2, F) or scales with thick coriaceous texture e.g., *R. lindleyi* and *R. maddenii* (Fig. 2, K; L). During winter, some species of *Rhododendron* leaves are curled due to exposure to stress such as frequent coverage of snow, drought, and extreme temperature. *Leaf* curl traits on *rhododendrons* may be due to the adaptation in serving as a desiccation-avoidance strategy and photoprotection role (Wang et al., 2008).

II. Variation in reproductive morphology

Calyx

Rhododendron species that grow under forest habitat have inconspicuous or reduced calyx except for *R. graffithianum*. This is because the young inflorescence bud associated with a fringe of hair-like structure overtakes the functions of a calyx (Cullen, 2005). However, a well-developed calyx is noticed in some taxa especially those species inhabiting a rocky habitat e.g., *R. lindleyi*, *R. maddenii*, *R. edgeworthii*, *and R. dalhousiae* var. *rabdotum.* Concerning the species in a marshland habitat, *R. ciliatum* has a well-developed calyx which is associated with scales and *R. thomsonii* appears to be unique with glabrous cup-shaped with incomplete calyx lobe. The *Rhododendron* of alpine habitats such as *R. setosum* and *R. anthopogon* is associated with the dense hairy structure.

Corolla

It is one of the most striking features observed in this genus with a wide variation of floral traits over the heterogeneous landscape and habitats. Based on the corolla shape, color, anther, and stigma position, 8 different floral types were recognized from the present study.

Floral type A (Plate 2, A; Table 3)

These are mostly white-colored flowers associated with scent and some flowers which are pinkish tinged with long corolla tube and subpatent to reflexed corolla lobe of intermediate length. The flower of this floral type has long exserted anther and stigma, e.g., *R. dalhousiae* var. *rhabdotum*, *R. edgeworthii*, *R. graffithianum, R. lindleyi*, and *R. maddenii*. These flower blooms early as compared with the rest of the flower types and are mostly observed in lower altitude 2000m to 2700 m asl. Within this elevation range, pollinators like species of *Hymenoptera*, *Diptera*, and

TABLE 3. List of collected *Rhododendron* species in Bhutan

Plant Species	Elevation (m)	Habit	Habitat	Tube length (mm) Mean ± SD	Opening diameter (mm) Mean ± SD	Anther length(mm) Mean ± SD	Stigma diameter (mm) Mean ± SD	Leaf length (mm) Mean ± SD	Collector No
R. aeruginosum Hook. f.	3500 - 4200	Krummholz	Alpine	24.8 ± 15.1	41.2 ± 35.2	2.9 ± 1.8	2.7 ± 2.0	107.8 ± 80.8	S.N 48
R. anthopogon D. Don	3600 - 4200	Prostrate scrub	Alpine	8.4 ± 5.9	17.1 ± 14.2	1.2 ± 0.6	1.0 ± 0.7	25.1 ± 17.3	S.N 46
R. setosum D. Don	3200 - 4300	Prostrate scrub	Alpine	3.5 ± 1.4	32.2 ± 24.5	2.4 ± 1.3	1.4 ± 1.0	14.8 ± 11.3	S.N 45
R. baileyi Balfour f.	3100 - 3900	Shrub	Alpine	5.8 ± 4.0	24.8 ± 19.2	2.9 ± 1.5	3.1 ± 1.4	30.6 ± 21.2	S.N 47
R. barbatum G. Don	3100 - 3800	Shrub	Forest	25.5 ± 15.7	48 ± 21.9	2.8 ± 1.6	2.2 ± 0.5	176 ± 82.3	S.N 05
R. campylocarpum Hook. f.	3300- 4300	Shrub	Forest	23.1 ± 17.8	45.2 ± 32.4	2.9 ± 1.8	1.9 ± 1.2	79.2 ± 50.6	S.N 29
R. ciliatum Hook. f.	2900 - 3200	Shrub	Marshland	31.5 ± 22.7	49.5 ± 28.0	4.9 ± 3.1	2.5 ± 2.0	68.3 ± 63.0	S.N 18
R. cinnabarinum Hook. f.	2500 - 3800	Shrub	Forest	20.4 ± 15.9	40.8 ± 22.1	2.5 ± 1.2	1.8 ± 1.2	59.1 ± 48.3	S.N 25
R. dalhousiae var. *rhabdotum* Balfour f. & copper	1500 - 2300	Shrub	Rocky slope	94.6 ± 78.1	97.1 ± 82.9	14.3 ± 11.5	5.9 ± 4.0	138.4 ± 125.8	S.N 43
R. edgeworthii Hook. f.	1800 - 2900	Shrub	Rocky slope	38.1 ± 26.3	96.2 ± 80.2	7.8 ± 5.5	4.5 ± 3.2	93.3 ± 72.3	S.N & K.S 13
R. keysii Nuttall	2900 - 3500	Shrub	Forest	18.0 ± 15.2	14.1 ± 9.1	2.1 ± 1.1	1.2 ± 0.7	105.8 ± 82.0	S.N 33
R. lanatum Hook.f.	3400 - 3900	Shrub	Forest	34.5 ± 27.2	57.8 ± 43.2	4.2 ± 2.5	2.5 ± 1.5	75.7 ± 14.3	S.N 44
R. lindleyi Moore	2000 - 2800	Shrub	Rocky slope	52.1 ± 44.9	90.2 ± 73.0	5.7 ± 5.2	5.9 ± 4.0	94.0 ± 53.4	S.N 04
R. neriiflorum Franchet	2300 - 3000	Shrub	Forest	26.0 ± 15.8	43.9 ± 38.9	3.3 ± 2.0	1.3 ± 1.0	117.5 ± 89.6	S.N 35
R. succothii Davidian	3200 - 3800	Shrub	Forest	24.2 ± 17.1	52.1 ± 38.2	2.4 ± 1.9	2.0 ± 1.1	119.5 ± 84.0	S.N 40
R. thomsonii Hook. f.	2900 - 3800	Shrub	Marshland	36.7 ± 25.1	64.9 ± 49.5	4.2 ± 2.3	2.8 ± 2.1	66.8 ± 46.1	S.N 37
R. triflorum Hook. f.	2600 - 3000	Shrub	Forest	15.2 ± 8.6	58.2 ± 32.1	3.1 ± 0.8	1.8 ± 0.9	59.0 ± 33.4	S.N & K.S 24
R. tsariense Cowan	3100 - 3900	Shrub	Forest	29.4 ± 26.5	45.6 ± 28.3	3.8 ± 2.7	2.0 ± 1.2	108.6 ± 94.1	S.N & K.S 15
R. virgatum Hook. f.	2000 - 3000	Shrub	Forest	16.1 ± 12.6	38.4 ± 23.2	3.6 ± 1.5	2.1 ± 1.1	49.4 ± 38.5	S.N & K.S 10
R. wallichii Hook. f.	3000 - 4100	Shrub	Forest	27.4 ±18.1	56.7 ± 26.7	4.7 ± 2.6	2.8 ± 1.7	156.6 ± 80.1	S.N & K.S 22
R. arboreum Smith	1900 - 3500	Tree	Forest	36.3 ± 24.6	53.5 ± 34.3	2.9 ± 1.8	2.4 ± 1.4	129.2 ± 89.1	S.N 30
R. argipeplum Balfour f. & Cooper	2600 - 3200	Tree	Forest	24.6 ± 20.5	42.8 ± 37.8	3.5 ± 2.0	7.2 ± 6.0	119.9 ± 110.3	S.N 02
R. falconeri Hook. f.	2500 - 3300	Tree	Forest	38.2 ± 30.9	52.1 ± 39.4	4.5 ± 3.0	6.8 ± 4.8	312 ± 241	S.N & K.S 17
R. grande Wight	1900 - 2600	Tree	Forest	48.2 ± 32.2	52.2 ± 38.2	5.4 ± 2.4	4.0 ± 3.3	159 ± 73.8	S.N 01
R. griffithianum Wight	1800 - 2500	Tree	Forest	51.9 ± 23.4	98.6 ± 97.7	5.8 ± 4.3	7.0 ± 4.6	118.7 ± 93.6	S.N & K.S 08
R. hodgsonii Hook. f.	3100 - 3500	Tree	Forest	32.2 ± 20.3	47.6 ± 31.4	3.2 ± 2.0	2.9 ± 1.9	293.7 ± 191.0	S.N 27
R. kesangiae Long & Rushforth	2600 - 3200	Tree	Forest	36.6 ± 25.6	53.3 ± 40.4	3.0 ± 2.0	4.6 ± 3.1	233 ± 187.5	S.N 28
R. maddenii Hook. f.	1800 - 2800	Tree	Rocky slope	46.2 ± 39.8	115.2 ± 99.2	5.2 ± 2.9	7.6 ± 6.4	116.5 ± 110.6	S.N 12
R. niveum Hook. f.	2900 - 3800	Tree	Forest	23 ± 15.4	37.9 ± 23.4	2.9 ± 1.6	1.5 ± 0.9	201.1 ± 142.8	S.N & K.S 21
R. wightii Hook. f.	3600 - 4200	Tree	Forest	31.0 ± 29.1	55.9 ± 45.2	3.3 ± 3.0	2.2 ± 1.9	128.9 ±92.0	S.N 26

Aethopyga are mostly found. During our pollination observation, we found only bees and insects visiting these floral types and rarely being visited by birds. Through the floral morphology of this floral type, birds could be a potential pollinator owing to its exerted stigma which is beyond the level of anther and wider corolla opening with a deep corolla tube where the bird can enter the corolla tube successfully (Campbell et al., 1996; Faegri and van der pijil, 1979; Willmer, 2011). Similar findings have been observed by Steven (1975) on the same floral type on the *Rhododendron* section *Vireya* in the Papuasia. One reason for the absence of bird pollinators of early flowering species could be due to low temperature during anthesis which might limit pollinator activity such as birds (Kudo, 1993). Therefore, further studies on these floral types are suggested.

Floral type B (Plate 2 B, Table 3)

Flower of this floral type is mostly associated with different range of colors and pigmentation on the base of the corolla tube. It is found at the elevation range of 2800 m to 3300 m except for *R. lanatum* and *R. wightii* which are found at 3700 m and 3900 m asl, respectively. During the pollination census, we observed that most of this floral type is visited by the species of Apidae, *Cyphipelta*, and *Lepidoptera*. Bee species of the family Apidae were found mostly visiting this floral type and birds are rarely found. Berry et al. (2017) reported that floral symmetry and the pigmentation pattern of a flower best suit for the bees for pollination. Additionally, the ultraviolet nectar guides offer a high visual acuity for bees to interact with this floral type (Dafni and Kevan, 1997).

Floral type C (Plate 2 C; Table 3)

It is a small tubular structure with an erect corolla lobe e.g., *R. keysii*. The stigma is ± erect and exserted, the stamen of almost the same length, which is usually oriented vertically, and this floral type appears to be one of the unique among the genera. It is found within the range of 3000-3500 m asl. The perching birds like Gould's Sunbird (*Aethopyga gouldiae*), Sunbird *(Aethopyga nipalensis)*, and Black-faced Laughingthrush (*Trochalopteron affine*) were observed as the common pollinators. It is suggested that tubular flowers of this species might have originally evolved for bird pollination where the bird's beak is suitable for probing foraging activities (Fenster 1991, Faegri and van der Pijl, 1979). Thus, the evidence on the present pollination survey suggests that birds exert selective pressure on this floral type.

Floral type D (Plate 2 D; Table 3)

It is interesting to note that this flower type is found only in Dagala alpine rocks and was not to be found in any other study sites. Due to time constraints, the field survey was limited to other geographical locations, and we expect its presence in other parts of Bhutan. However, a further survey is suggested to confirm its validity. This distinct flower is associated with a short and round corolla tube with deep colored blotches on the adaxial part of the corolla lobe. It grows on the elevation range of 3200 m to 3700 m asl. The corolla lobe is arranged slightly perpendicular to the axis and looks almost like a polypetalous, e.g., *R. baileyi*. This flower has exceptional floral traits with included stigma and surrounded by the short, exerted stamens. We observed that the bumblebees of the *genus Bombus* were the only active pollinators (Plate 3, C), and birds are rare to be found.

Floral type E (Plate 2 E; Table 3)

The flower is usually a bowl-shaped flower with 8-9 corolla lobes with 12-15 stamens of different lengths. It is found at 2800 m to 3600 m asl. e.g., *R. falconeri*, *R. grande*, *R. hodgsonii*, and *R. kesangiae*. This floral type is usually found in the understory of the coniferous forest with a small amount of nectar. It could be reasoned that the growing

understory of the coniferous forest might have limited the plant productivity and thus large amount of nectar production is restricted. We propose that birds could be the potential pollinator due to its 'mechanical fit' between the bird and the flower (Huang et al., 2017). Similarly, we found birds like Black-faced laughing thrush (*Trochalopteron affine*), *Whistler's warbler* (*Phylloscopus whistleri*), and R*ufous sibia* (*Heterophasia capistrata*) frequently visiting this flower type (Plate 3, G). Other pollinators like bees and insects were also found during clear sunny days however, due to harsh weather conditions experiencing throughout, bees and insects remain inactive most of the time.

Floral type F (Plate 2 F; Table 3)

It is usually red tubular-campanulate which has conspicuous nectar content and found within an elevation range of 3000 m to 3700 m asl, e.g., *R. arboreum*, *R. argipeplum*, R. *barbatum*, *R. succothii*, and *R. thomsonii*. During our pollination census, we have observed that this flower type is visited by bees and birds of different visiting intervals. In the early morning, the birds such as Gould's Sunbird (*Aethopyga gouldiae*), Green-tailed Sunbird *(Aethopyga nipalensis)*, Lesser shortwing (*Brachypteryx leucophris*), Bar-throated Siva (*Chrysominla strigula),* Black-faced Laughingthrush (*Garrulax affinis*), Whistler's warbler (*Phylloscopus whistleri*), *and* white-throated laughingthrush *(Pterorhinus albogularis)*. Bumblebees and honeybees were also observed as frequent visitors of this floral type. The bees visit these floral types only during a calm and sunny day. In some species like *R. thomsonii* we observed that flies also visit the flower during a sunny day. A similar observation has been described by Basnett et al., (2019) of the same species in eastern Sikkim Himalaya. Further scientific inquiry on the Dipteran species as a role of pollinators should be investigated since it is purely neglected in terms of pollinators. We suggest that the intermediate blossom type, which is considered as an advanced in blossom organization (Faegri and van der pijl, 1979) might have evolved as a strategy in attracting wide diversity of pollinators where pollinators of both long and short proboscis can be accessible for pollen and nectar.

Floral Type G (Plate 2 G; Table 3)

It is slightly tubular with a small corolla tube opening and it is the only species where both stamens and stigma remain included in the corolla tube, e.g., *R. anthopogon*. It grows in the alpine region 3800 above till 4700 m asl, in the form of a creeping mat. In this region, unpredictable and harsh climatic conditions such as snow, frost, and strong winds restrict the bird pollinators. Therefore, this floral type depends heavily upon the bees and insects as the pollinator in the alpine region (Pellissier et al., 2010, Smith et al., 2008). However, we propose that this flower type is pollinated by an insect with long proboscis because of its unique morphological adaptation as seen in (Plate 3, J). This hypothesis requires further experimental study to investigate the potential pollinator of this flower type.

Flower type H (Plate 2 H; Table 3)

This flower type has a short corolla tube or funnel-shaped with long and reflexed corolla lobe e.g., *R. setosum*, *R. triflorum*, and *R. virgatum*. *Rhododendron virgatum* and *R. triflorum* are found between 2000 m to 3000 m asl under-canopy of pine trees. *R. setosum* which grows above 3800 m is the only plant species that ends on the alpine gradient. Bumblebees, flies, and insects were found to the prominent pollinators and bird abundance felt drastically low from 4000 m and above (Plate 3, K). Those alpine plants need more attention since they rely heavily on single guilds of pollinator and the survival of species might be threatened if the environment becomes unfavorable to the pollinators due to climate change (Berry et al., 2017).

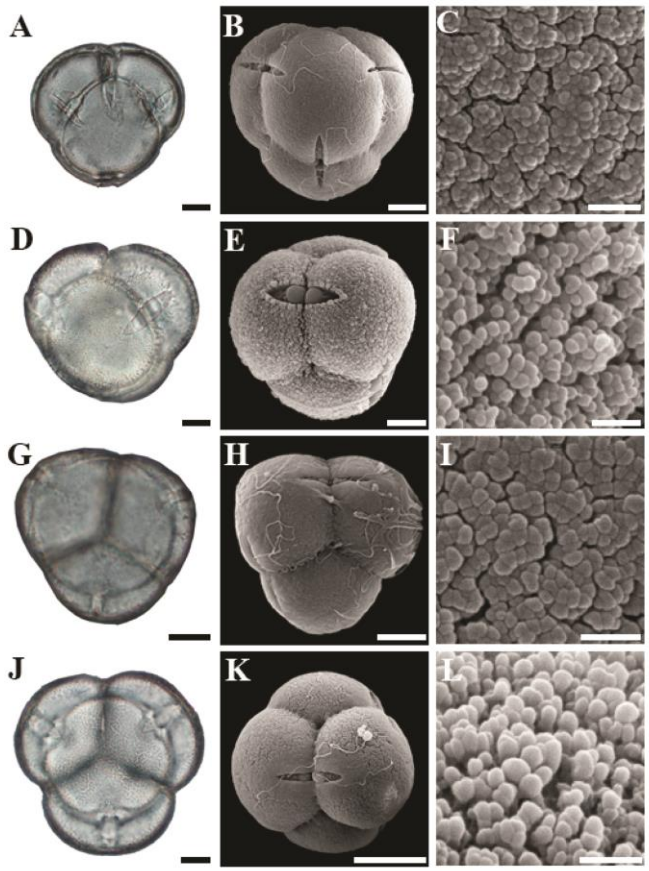

FIGURE 6. LM and SEM micrographs of *Rhododendron* pollen. **A-C** (*R. aeruginosum*), **D-F** (*R. baileyi*), **G-I** (*R. barbatum*), **J-L** (*R. cinnabarinum*); **A**, **D**, **G,** and **J** from LM (scale bar = 10 µm), **B**, **E**, **H**, and **K** from SEM (scale bar = 10 µm); **C**, **F**, **I** and **L** show gemmate ornamentation from SEM (scale bar = 1 µm).

Pollens

Pollens of all *Rhododendron* species are arranged in tetrahedral tetrads along with the viscin thread (Figs. 6 and 7; Table 2). This pollen presentation signifies that rhododendrons are zoophilous pollination syndrome taxa. However, no significant variation in tetrad size was observed from the selected plant taxa. We suggest that the tetrads presentation of pollen might have evolved to enable the chances of pollination and the viscin thread of pollen tetrads might have played an important role in the pollen removal process (Sarwar and Takahashi, 2013, Song et al., 2019). Moreover, the viscin thread helps to attach pollen at the edge of the open pollen sac and avoid premature falling off pollen (Hesse et al., 2000). Considering the palynological study of this genus *Rhododendron*, it has been reported that it is one of the relictual plant taxa with pollen tetrad presentation without viscin thread during the cretaceous period. Later during Eocene, viscin thread is thought to be established as an advanced trait that connects the pollen (Zetter and Hesse et al., 1996). Therefore, it is plausible to infer that pollen vectors such as bees, birds, and insects might have evolved during this era. Some scientific studies suggest that the structure of the viscin

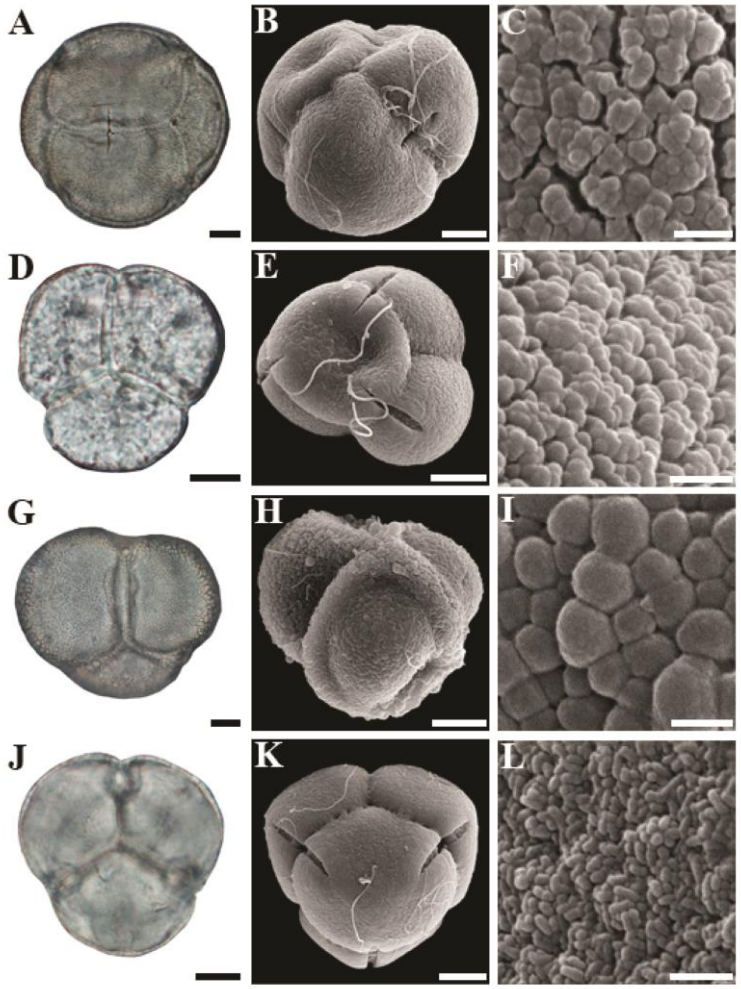

FIGURE 7. LM and SEM micrographs of *Rhododendron* pollen**. A-C** (*R. lindleyi*), **D-F** (*R. setosum*), **G-I** (*R. thomsonii*), and **J-L** (*R. wightii*); **A**, **D**, **G** and **J** from LM (scale bar = 10 µm), **B**, **E**, **H,** and **K** from SEM (scale bar = 10 µm); **C**, **F**, **I** and **L** show gemmate ornamentation from SEM (scale bar = 1 µm).

thread varies between the pollinators. According to Skvarla et al., (1978), the viscin thread in Onagraceae varies between the bee and bird pollinated taxa. For bird and moth pollinated taxa it is accompanied by rough or beaded viscin threads whereas for bee-pollinated taxa it is associated with smooth viscin thread. Although *Rhododendron* taxa are associated with bee and bird pollination yet the palynological study of *Rhododendron* taxa in Bhutan is extremely limited. Further study is encouraged to test the structure of the viscin thread of bee-pollinated and bird-pollinated taxa of *Rhododendron*.

Fruits and seeds

The matured fruits are woody structure with minute hairy like structure, glabrous and sometimes it is associated with scales. The capsule may be slightly cylindrical, straight, or curved with varying sizes ranging from 10 mm in *R. setosum* to 40 mm in *R. hodgsonii*. The capsule raptures (septicidal capsules)

TABLE 4. Pollen morphology of selected *Rhododendron* species

Taxa	Polar axis (µm) Mean ± SD	Equatorial axis (µm) Mean ± SD	P/E	Shape	Aperture	Ornamentation	Exine thickness (µm) Mean ± SD
R. aeruginosum	28.78±3.89	39.02±2.25	0.737570	oblate	tricolpate	gemmate	1.09 ± 2.47
R. baileyi	28.95±4.40	37.65±3.26	0.768924	suboblate	tricolpate	gemmate	1.09 ± 2.47
R. barbatum	21.02±1.90	29.98±1.45	0.701134	oblate	tricolpate	gemmate	0.61 ± 1.84
R. cinnabarinum	31.22±2.80	40.97±2.35	0.762020	suboblate	tricolpate	gemmate	0.73 ± 1.82
R. lindleyi	33.50±3.53	46.65±3.51	0.718113	oblate	tricolpate	gemmate	1.16 ± 2.65
R. setosum	19.72±3.70	27.76±3.77	0.710374	oblate	tricolpate	gemmate	0.69 ± 1.48
R. thomsonii	27.34±5.03	37.00±5.25	0.738918	oblate	tricolpate	gemmate	0.82 ± 2.51
R. wightii	24.74±3.01	35.82±3.30	0.690675	oblate	tricolpate	gemmate	0.51 ± 1.63

Note: ; SD=Standard deviation

when fully matured and the seeds are arranged in the narrow septum chamber where they escape. Seeds of *Rhododendron* species are relatively small and mainly dispersed by the wind. Through morphological study, the seed can be placed in two categories.

Seed type 1

The seed is prominent with oval or slightly cylindrical shape and a large seed surface area, which is associated with conspicuous lateral wings all around e.g., *R. falconeri*, *R. kesangiae*, etc. (Fig. 5, 1A; 1D; Table 4). The basal and apical wings are irregularly dissected. The seed of this plant taxa is usually found growing on forests and rocky cliff habitats. We observed that *Rhododendron* species of rocky cliff habitat experiences high wind velocity and remain foggy most of the time as compared to the plant taxa of forest habitat. While concerning its distribution, under forest habitat the plant grows as a crowded stand while the plant grows sparsely under rocky cliff habitats. It could be inferred that such distribution and plant establishment under different habitat might be plausible due to the dispersal ability and the seed developmental allometry. According to Wang et al., (2014), seed traits such as seed mass, seed surface area, and seed wing length of *Rhododendron* species are found to be highest on rocky slope habitat. *Rhododendron* species on the rocky slope habitat are found to be less abundant and thus such seed traits might have attributed to the dispersal and colonization ability.

Seed type 2

The seed is elongated, without wings but rather forming tail-like appendage tapering to both the ends (Fig. 5, 2A; 2B; 2C; 2D, Table 4). This seed type is mostly associated with the alpine plants that grow above the tree line e.g., *R.* anthopogon, *R. lanatum*, and *R. setosum*. The resource constraints in the alpine region may allocate into smaller seeds with low seed mass so that the wind could help in the dispersal. Further, the small seed size of the alpine plants may be due to the short growing season, which might have reduced the time for seed growth (Guo et al., 2010, Wang et al., 2014). We suggest that such seed morphology might be due to selective pressure over a long ecological time.

Conservation

During our survey, we have observed that the natural habitat of rhododendrons was disturbed by developmental activities such as the widening of as east-west highway, natural cause, and other anthropogenic activities. Habitat disturbances by cutting down the *Rhododendron* trees which are best known for their fuel especially by the herders in the alpine region have put pressure on these plants. Additionally, some alpine species such as *R. anthopogon* and *R. setosum* are used in

the process of making incense sticks. Presently, Bhutan has one *in situ Rhododendron* garden at Phrumsengla National Park and one *ex-situ* cultivation in Royal Botanical Park in Lamperi, near Dochula. Above all, the wild population of *Rhododendron* in Bhutan belongs to national parks and sanctuaries. However, we observed that *R. ciliatum, R. dalhouse* var. *rhabdotum, R. niveum,* and *R. succothii* are rare and endangered. Therefore, to counter this, creating awareness and establishing *in vitro* micropropagation research program could be initiated to conserve the endangered species and protect the existing gene pool of rhododendrons before it gets extinct.

CONCLUSION

Thirty *Rhododendron* species from different geographical locations of Bhutan Himalayan ranges reveals a significant floral and seed morphological variation. We believe that the evolution of floral variation of the genus *Rhododendron* could be due to the pollinator selection interaction called pollination syndrome. However, for some plant species, the hypothesis does not agree with the pollination syndrome concept. Hence, it remained a subject of controversy. Bees and birds were found to be specific pollinators to some of the species and some species invite general pollinators including flies. The pollinators such as butterflies, moths, and bats were not explored due to time constraints. Therefore, a further experimental study is strongly encouraged to test this hypothesis in *Rhododendron* flowers. There is paucity in the scientific inquiry about this genus, its pollination biology, and ecology in Bhutan. Thus, our research study would encourage and stimulate further investigation of this plant genus.

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APPENDIX: PLATES

PLATE 1. Different habits of *Rhododendron*. **A,** Tree; **B**, Scrub; **C,** Krummholz; **D,** Creeping scrub

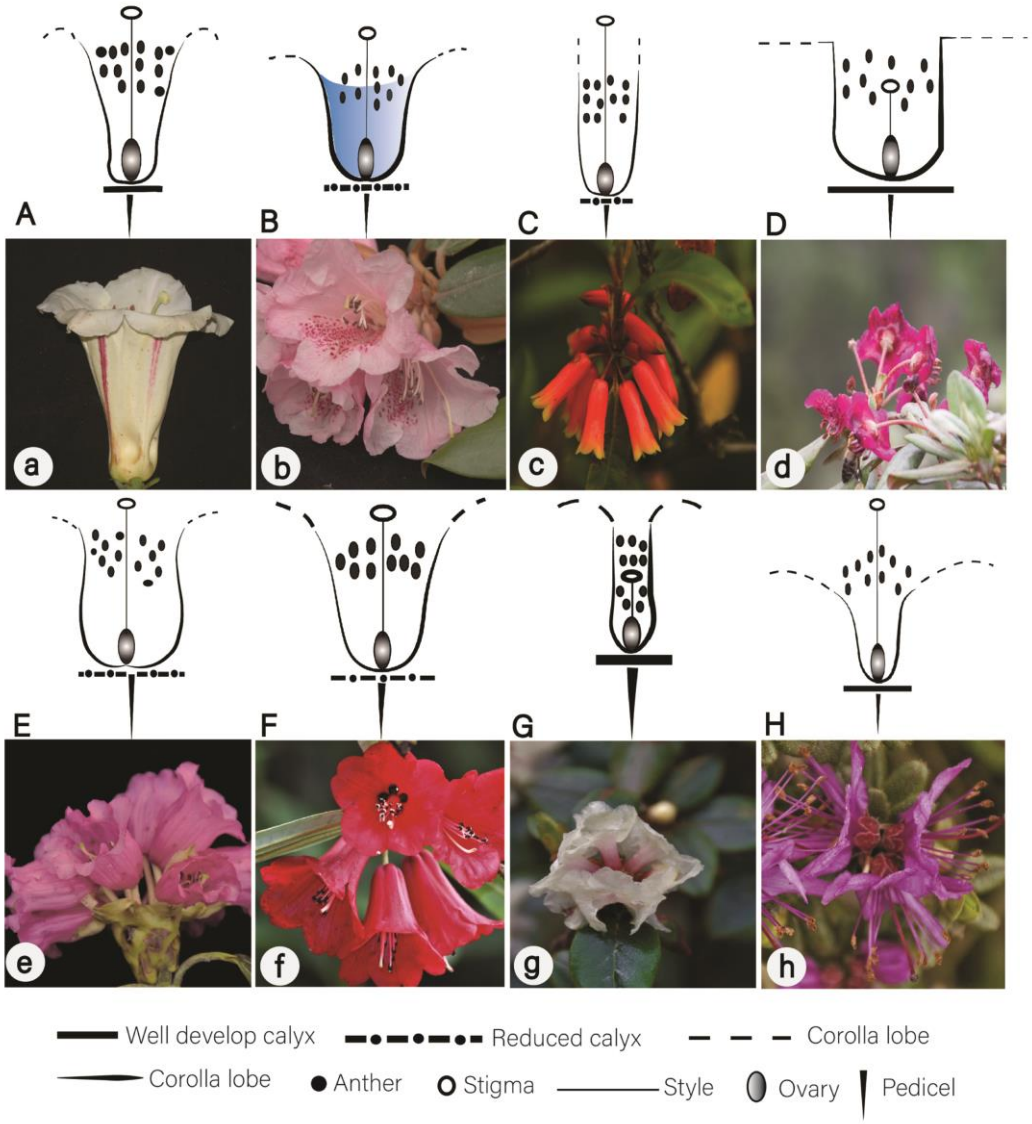

PLATE 2. Floral types of genus *Rhododendron* in Bhutan Himalayan ranges. Capital letters represents the flower type and small letters represents the illustrations. **(A), (a),** Blossom Type A; **(B), (b)**, Blossom Type B; **(C), (c),** Blossom Type C; **(D), (d),** Blossom type D; **(E), (e),** Blossom Type E; **(F), (f),** Blossom type F; **(G), (g),** Blossom Type G; **(H), (h),** Blossom Type H.

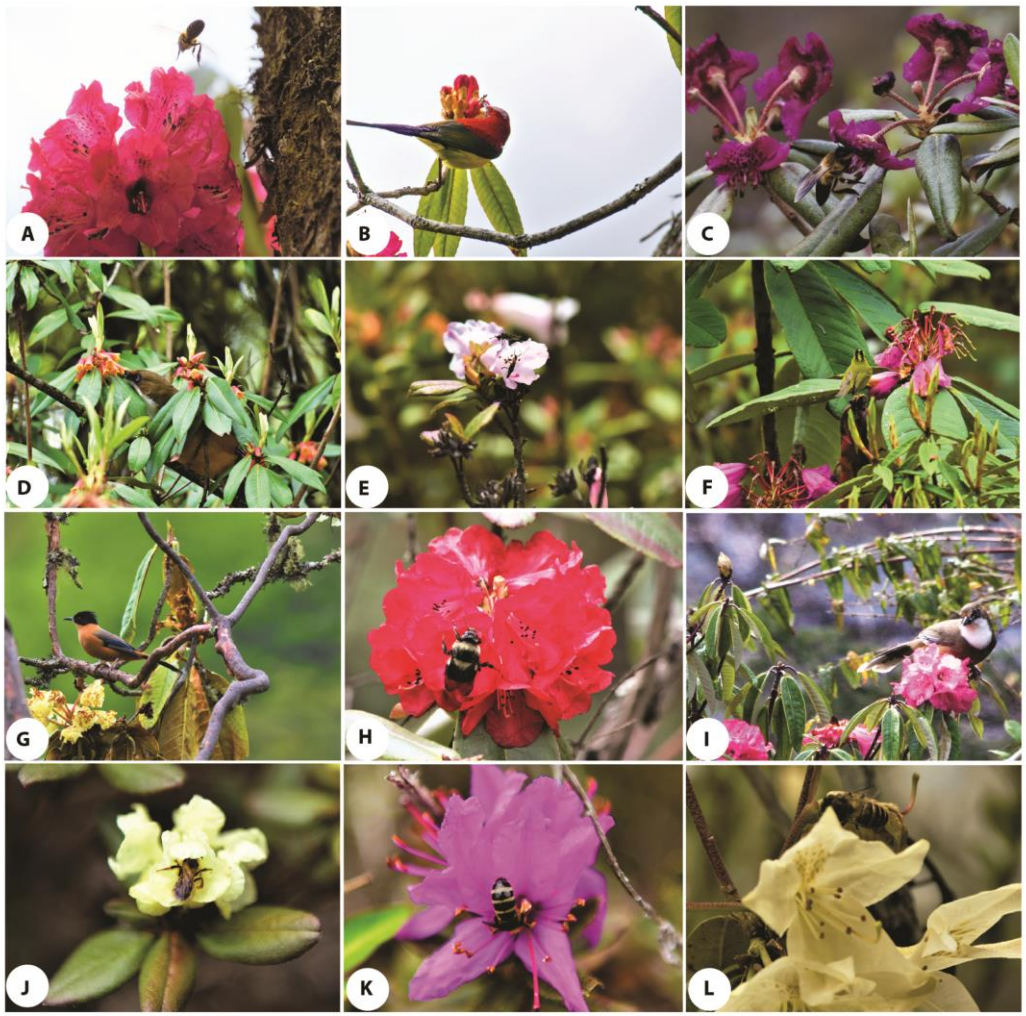

PLATE 3. Pollinator's interaction of *Rhododendron* species studied in the different geographical locations of Bhutan Himalayan ranges. **A,** Bees visiting on tubular campanulate flowers (Blossom Type F) of *R. arboreum*; **B,** Gould's sunbird (*Aethopyga gouldiae*) visiting on *R. Kendrickii* (Blossom Type F); **C,** *Bombus sp*. visiting on flower of *R. baileyi* (Blossom Type D*)*; **D,** Black-faced Laughingthrush (*Trochalopteron affine*) visiting on *R. keysii* (Blossom Type C); **E,** *Diptera sp.* on *R. ciliatum*; **F,** *Whistler's warbler* (*Phylloscopus whistleri*) on *R. kesangiae* (Blossom Type F); **G,** *Rufous sibia* (*Heterophasia capistrata*) on *R. falconerii* (Blossom Type E); **H,** *Bombus* sp. on *R. succothii* (Blossom Type F); **I**, *White-throated Laughingthrush (Pterorhinus albogularis)* visiting on *R. arboreum;* **J,** *Diptera* sp. visiting on *R. anthopogon* (Blossom Type G); **K,** *Bombus* sp. visiting on *R. setosum* (Blossom Type H); **L,** *Apis* sp.visiting on *R. triflorum* (Blossom Type H)