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RESEARCH ARTICLE

Exploring the role of heterosis in improvement of floral and vegetative traits in *Chrysanthemum*

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Abstract

In the present study, eight genotypes of *Chrysanthemum* were crossed and heterosis was assessed in 28 F1 hybrids. The studies were conducted at the research plot of BTCC (Biotechnology Cum Tissue Culture Centre), Department of Floriculture and Landscaping, Odisha University of Agriculture & Technology (OUAT) Bhubaneswar. The expression of heterosis in F1 hybrids of *Chrysanthemum* was evaluated in terms of their vegetative and floral attributes. Controlled crossing half-diallel mating design was followed and F1 hybrids were analysed for their performance. The results were compared to parental lines and the extent of heterosis was determined. Significant variation was noted for most characters. The hybrid (ACC-1 ×UHFS-68) was found to exhibit a significant negative heterosis (RH, MP) for the characters such as plant height, days to flower bud initiation and days to final bloom while a significant positive effect of heterosis was noted for flower yield. The cross (Shova × Arka Kirti) exhibited significant positive heterosis for the character flowers per plant and flower yield and negative heterosis was noted for the character days to flower bud initiation. Hybrid (Shova× ACC-1) was found superior to parent in terms of the number of flowers per plant. Both the hybrids showed superiority for this trait. Results revealed that the performance of F1 hybrids were superior to their parents for vegetative and floral attributes.

Keywords: chrysanthemum; heterosis; F1 hybrids; half-diallel; hybrid vigour; ornamental plants

Introduction

Chrysanthemum (*Chrysanthemum morifolium Ramat.*) is one of the most popular ornamental plants known for its aesthetic appeal and economic importance. Some researchers have found that East Asia is the centre of origin of modern-day cultivated *Chrysanthemums* (1, 2), while others suggested that they are localised to Asia and Northeastern Europe (3). The cultivation of *Chrysanthemum* is carried out in various forms such as cut flowers, potted plants and garden varieties. The genetic diversity within *Chrysanthemum* offers immense potential for breeding that can be done with an aim of developing superior hybrids.

Genetic diversity in any crop is crucial for developing novel, desired forms through breeding and selection. Hybridization is one of the important breeding strategies which is based on knowledge of diversity and its response to natural/human selection. *Chrysanthemum morifolium* is available in a variety of colours and has been developed through complicated interspecific crossings across various species by open pollination, indiscriminate inter-varietal hybridization, spontaneous and artificial mutation and chimaera selection and management. Heterosis, or hybrid vigour, is a phenomenon where F1 hybrids outperform their parents for various traits. Heterosis in hybrid breeding is a significant success in plant breeding (4).

Heterosis is important in hybrid production, especially for features influenced by non-additive gene activity (5). Heterotic group can be defined as a collection of related or unrelated genotypes from the same or different populations that exhibit similar combining ability and heterotic response when crossed with genotypes from other genetically distinct germplasm groups (6). Heterosis is done in three ways mid-parent, better-parent and standard. In quantitative genetics, mid-parent heterosis is a hybrid's superiority over the mean of its parents (7). Average or relative heterosis occurs when the hybrid outperforms the mid-parent (8). Heterosis is a hybrid's advantage over the best parent, assessed in comparison to the superior or better parent. The hybrid's domination over the better parent resulted in superiority (9). Standard heterosis refers to a hybrid's higher performance in terms of desired features over a standard commercial hybrid variety (10). Standard heterosis is crucial for developing superior hybrids over existing high-yielding varieties. Horticultural crops can harness heterosis can be done in horticultural crops to get enhanced growth rate, high yields, improved stress tolerance and superior aesthetic traits. Thus, heterosis can prove useful in the floriculture industry as new breeds can be developed. Understanding the extent and expression of heterosis in *Chrysanthemum* hybrids can guide breeders in developing new varieties with desirable characteristics. Therefore, this study aims to estimate the effect of heterosis on floral and vegetative parameters, flower yield and how heterosis can prove useful in developing superior, high-yielding varieties.

Materials and Methods

The present investigation was carried out at the research field of BTCC, Department of Floriculture and Landscaping, OUAT, Bhubaneswar, during the *Rabi* season of 2019-20, 2021-22 and 2022-23. Eight cultivated varieties of *Chrysanthemum* viz., Shova, ACC-1, SS, Arka Kirti, Pusa Chitrakshya, BCKV 123, UHFS -56, UHFS-68 were taken for for hybridization. The hybridization was carried out in a half-diallel manner (each parent is mated with other parent excluding self and reciprocal) and as a result 28 F1 crosses were carried out and hybrids evolved (excluding the reciprocals) were studied. Cuttings were raised during the rainy season and then transplanted in polybags after root development. Practices such as pinching, disbudding and fertigation were carried out for raising the plants. Observations were recorded at an interval of 15 days for vegetative and flower yield attributes. The parental lines were selected based on their distinct morphological and phenotypic traits. The diverse lines were chosen to maximize genetic variability and get maximum effect of heterosis in F1 hybrids. The parameters viz., plant height, number of leaves per branch, number of branches per plant, stalk length, days to flower bud initiation, days to final bloom, number of flower buds per plant, number of flowers per branch and number of flowers per plant were recorded in five randomly selected plants and their average was calculated. The heterosis (relative heterosis, heterobeltiosis) results were interpreted as as percentage increase or decrease of F1 hybrids (11). The visualization of graphs was done using R Studio and data analysis was carried out using software TNAUSTAT.

Hybridisation process

Controlled cross-pollination was carried out between the selected parents to develop F1hybrids. The hybridisation process involved :

- Emasculation of the flowers to prevent self-pollination.
- Hand-pollination using pollen from the selected male parent.
- Bagging the pollinated flowers to ensure controlled fertilization.

A total of 28 F1 hybrids were developed through this process and were studied for heterosis in F1 generation.

Results and Discussion

The analysis of variance for the traits studied is given in Table 1. The variance due to genotypes was found significant for all the characters studied, indicating sufficient trait variability. Tables 2 to 4 show the range of heterosis and the number of crosses displaying significantly positive and negative heterosis over the standard check (BCKV 123). Negative heterosis is desired for some traits, such as days to first bud initiation, flowering duration and plant height, whereas positive heterosis is desirable for other characteristics like flower yield, number of flowers/branch and number of branches per plant.

Of the twenty-eight hybrids, twenty-five hybrids were found to have significant positive heterosis ranging from (3.57 to 16.94) for plant height while only one hybrid had negative heterosis (-4.12), (ACC-1 ×UHFS-68), which can be exploited for creating dwarf hybrids. The hybrids showing heterosis in a negative direction could be used for flower beds, pot plants and border plants (12). In *Chrysanthemum*, dwarf hybrids are used as pot mums, so negative heterosis is efficient.

The heterosis over better parent (heterobeltiosis) ranged from (-7.08 to 11.60), while for the standard check, maximum and minimum heterosis was found in the hybrids (ACC1×BCKV123), (Pusa Chitrakshya×UHFS-68) respectively (Table 3). Hybridization of dwarf cultivars with wild species by mixed or open pollination allowed for the development of new *Chrysanthemums* (13). Groundcover *Chrysanthemums* were developed over generations of hybridization and selection and several excellent cultivars were successfully introduced for urban horticulture (14).

The relative heterosis showed maximum and minimum values in the hybrids (ACC-1×UHFS-68) (34.37) and (Pusa Chitrakshya×UHFS-56) (2.12) for the number of branches per plant. About nineteen hybrids recorded significant positive heterosis (Table 2). A substantial degree of relative heterosis for the character number of branches per plant was reported in China aster (15). The heterobeltiosis ranged from (-13.25 to 23.83) and nine hybrids recorded significant positive heterosis over the better parent (Table 3). The standard heterosis ranged from (-12.22 to 25.30) (Table 4). Identical results were also reported in China aster (16) and marigold (17). A significant positive heterosis was found in the fourteen hybrids over the standard variety, similar results were reported in marigold (18, 19).

Among the 28 hybrids, twenty-one hybrids exhibited

Table 1. Analysis of variance for different parameters of *Chrysanthemum* in F1 hybrids

Source	Df	Plant height (cm)	Number of branches	Number of leaves per branch	Stalk length (cm)	Days to flower bud initiation	Days to final bloom	Number of flower buds per plant	Number of flowers per branch	Number of flowers per plant
Genotype	35	25.7013**	6.0665 **	2.9126 **	10.825 **	16.9862 **	27.0113**	21.3118 **	0.5188**	7.4027**
Error	72	16.1936	0.6729	1.9333	19.0982	6.2223	5.3685	7.0983	0.3064	4.1922
Total	107	41.8949	6.7394	4.8459	29.9232	23.2085	32.3798	28.4101	0.8252	11.5949

*Significant at P=0.05, **Significant at P=0.01

Table 2. Estimation of relative heterosis for vegetative and floral attributes

Hybrids	Plant height	No. of branches	No. of leaves/stem	Stalk length	Days to flower bud initiation	Days to final bloom	No. of flower buds/plant	No. of flowers/ branch	No. of flowers/plant
Shova×ACC-1	4.66**	20.41**	-4.03*	-15.61**	-11.38**	-4.31**	15.17*	7.30	2.89**
Shova×SS	11.44**	-2.61*	0.61	-4.26	-4.97	-1.00	31.88**	12.81	2.53**
Shova×Arka Kirti	5.38**	-1.33	0.52	3.93	-7.51*	0.01	8.94	16.39	3.53**
Shova×Pusa Chitrakshya	10.77**	0.25	-2.44	-2.97	-11.46**	2.05	21.99**	5.53	0.97
Shova×BCKV123	8.37**	5.00**	-1.10	8.60*	-3.24	2.21*	24.65**	20.30	2.17*
Shova×UHFS 68	4.94**	11.11**	-6.82**	11.49**	-8.34*	-1.47	21.09**	31.48**	0.19
Shova× UHFS56	16.94**	2.75*	-9.67**	2.34	-3.91	0.72	-8.04	-3.03	-1.01
ACC-1×SS	9.84**	17.41**	-2.29	5.33	-3.09	-4.86**	16.88**	3.24	0.51
ACC-1×Arka Kirti	3.57*	12.42**	-1.89	3.86	-8.38*	-4.43**	2.40	24.26*	2.67**
ACC-1×Pusa Chitrakshya	5.17**	20.43**	-4.92*	13.16**	-7.26*	-4.01**	16.83**	1.13	1.13
ACC-1×BCKV123	7.29**	13.29**	0.19	16.01**	-6.61*	-2.71*	16.94**	16.47	3.12**
ACC-1×UHFS68	-4.12**	34.37**	-7.31**	13.37**	-6.10	-6.99**	29.63**	38.81**	0.94
ACC-1×UHFS56	7.70 **	21.05**	-3.29	4.17	-8.92**	-8.74**	-0.23	6.93	1.27
SS×Arka Kirti	7.35 **	3.22 **	2.33	5.79	-6.34	-5.77**	-27.68**	-8.70	1.72
SS×Pusa Chitrakshya	12.87**	16.60 **	0.04	13.77**	-9.60**	-3.96**	-2.43	-36.28**	-0.54
SS×BCKV123	9.70 **	24.56 **	0.55	16.94**	-6.64	-2.44*	19.08**	-34.78**	0.83
SS×UHFS68	10.66**	-1.67	-3.70	5.13	-10.63**	-6.35**	25.40**	-20.00	-2.14*
SS×UHFS56	5.27 **	-1.88	-.39**	3.59	-18.46**	-9.43**	6.74	-25.73**	-2.91**
Arka Kirti×Pusa Chitrakshya	4.88 **	10.67**	-3.90	10.60**	-8.19*	-3.33**	3.11	-8.26	-1.00
Arka Kirti ×BCKV123	3.58*	-7.54**	1.39	15.33**	-7.72*	-4.04**	-4.51	27.27*	2.56*
Arka Kirti ×UHFS68	-0.05	1.02	-2.99	9.35*	-13.92**	-3.77**	-17.37**	44.74**	-1.01
Arka Kirti ×UHFS56	1.84	3.58**	-4.24*	-4.10	-10.97**	-6.34**	-26.28**	15.66	-1.10
Pusa Chitrakshya×BCKV123	6.33**	1.59	2.82	11.29**	-6.88*	-1.78	19.73**	-0.31	1.92
Pusa Chitrakshya ×UHFS68	11.96**	11.70**	-1.71	12.10**	-6.07	-4.60**	9.70	1.99	-0.04
Pusa Chitrakshya ×UHFS56	11.94**	2.12*	-5.56*	14.06**	-11.54**	-5.79**	7.74	-21.23**	-1.23
BCKV 123×UHFS68	12.21**	22.28**	7.01**	15.25**	-1.88	-2.94**	26.20**	9.65	4.31**
BCKV 123×UHFS56	12.27**	11.74**	4.29	9.06*	-1.20	2.34*	-3.40	-26.78**	2.12*
UHFS68×UHFS56	3.81*	6.19**	-1.57	8.47*	-5.19	-0.93	-0.77	-11.97	-0.51
SE	**0.68**	**0.13**	**0.48**	**0.80**	**1.32**	**0.79**	**1.23**	**0.22**	**0.61**

*Significant at P=0.05, **Significant at P=0.01

Table 3. Estimation of heterobeltiosis (BP-better parent heterosis) for vegetative and floral attributes

Hybrids	Plant height	No. of branches	No. of leaves/stem	Stalk length	Days to flower bud initiation	Days to final bloom	No. of flower buds/plant	No of flowers/ branch	No. of flowers/ plant
Shova×ACC-1	0.23	13.72**	-4.90*	-18.89**	-16.17**	-7.25**	14.06	5.00	2.31*
Shova×SS	3.01	-13.25**	-1.30	-10.71*	-6.38	-3.61**	29.44**	8.89	0.19
Shova×Arka Kirti	-2.17	-14.76**	-0.20	-6.65	-9.70*	-3.67**	-9.58	15.52	1.96
Shova×Pusa Chitrakshya	1.33	-8.98**	-6.30**	-3.13	-15.56**	-2.26	13.63*	-10.97	0.32
Shova×BCKV123	5.08 **	-5.99**	-8.88**	6.35	-7.38	-1.55	24.09**	19.40	-0.48
Shova×UHFS 68	-2.47	-2.57*	-9.72**	10.35*	-14.14**	-7.75**	20.52**	12.84	-0.41
Shova× UHFS56	10.25**	-11.48**	-12.56**	-4.37	-11.06**	-6.39**	-17.28**	-11.66	-1.20
ACC-1×SS	5.84**	-0.52	-4.99*	2.08	-7.01	-5.30**	13.64	1.81	-2.33*
ACC-1×Arka Kirti	0.25	-7.43**	-3.47	-3.22	-11.30**	-5.03**	-14.33**	20.71	0.55
ACC-1×Pusa Chitrakshya	0.25	3.88**	-9.48**	8.57	-8.05*	-5.19**	9.82	-13.13	-0.09
ACC-1×BCKV123	5.92**	-3.54**	-8.46**	9.28*	-7.75*	-3.33**	16.33*	13.14	1.02
ACC-1×UHFS68	-7.08**	12.20**	-10.98**	10.04*	-7.08	-10.25**	27.78**	17.00	-0.24
ACC-1×UHFS56	5.95 **	-0.58	-7.20**	1.16	-11.00**	-12.61**	-9.47	-0.61	0.50
SS×Arka Kirti	6.85 **	-0.33	1.10	1.58	-7.19	-6.80**	-40.85**	-12.50	0.91
SS×Pusa Chitrakshya	11.60**	14.14**	-2.11	5.93	-12.53**	-5.57**	-10.67	-44.62**	-2.20*
SS×BCKV123	4.41 *	23.83 **	-5.69*	6.96	-9.33*	-3.51**	16.37*	-37.50**	-3.96**
SS×UHFS68	10.00**	-3.40 **	-4.92*	-1.01	-15.10**	-10.03**	23.66**	-33.33**	-3.81**
SS×UHFS56	3.08	-5.55 **	-9.63**	3.37	-23.46**	-13.65**	-5.56	-30.06**	-4.95**
Arka Kirti×Pusa Chitrakshya	3.22	4.70 **	-7.06**	-0.81	-10.37**	-3.91**	-9.01	-23.08**	-1.87
Arka Kirti ×BCKV123	-0.98	-11.22**	-5.97 *	1.69	-9.57*	-4.05**	-20.45**	27.27*	-1.56
Arka Kirti ×UHFS68	-0.18	-0.73	-5.35 *	-0.88	-17.50**	-6.57**	-31.67**	25.00*	-1.92
Arka Kirti ×UHFS56	0.18	3.24**	-6.65**	-8.11*	-15.71**	-9.76**	-32.69**	4.66	-2.41*
Pusa Chitrakshya×BCKV123	0.13	0.03	-1.54	9.16	-7.24	-2.36	12.00	-16.41*	-1.33
Pusa Chitrakshya ×UHFS68	10.06**	7.46**	-2.60	10.77*	-7.83*	-6.83**	1.73	-23.90**	-0.08
Pusa Chitrakshya ×UHFS56	8.41**	-3.69**	-6.33*	6.42	-14.28**	-8.70**	3.74	-27.69**	-1.67
BCKV 123×UHFS68	7.40**	19.43**	1.59	11.73*	-4.08	-5.76**	25.04**	-5.30	1.02
BCKV 123×UHFS56	9.05**	6.96**	-0.91	-0.06	-4.62	-1.39	-12.76*	-33.74**	-0.71
UHFS68×UHFS56	2.25	4.02**	-1.66	2.34	-6.39	-1.70	-11.11	-30.06**	-0.91
SE	**0.79**	**0.15**	**0.55**	**0.93**	**1.53**	**0.92**	**1.42**	**0.26**	**0.70**

*Significant at P=0.05, **Significant at P=0.01

Table 4. Estimation of standard check heterosis for vegetative and floral attributes

Hybrids	Plant height	No. of branches	No. of leaves/ stem	Stalk length	Days to flower bud initiation	Days to final bloom	No. of flower buds/plant	No of flowers/ branch	No. of flowers/ plant
Shova×ACC-1	2.86	-10.08**	14.94**	-8.23	-14.06**	-8.44**	15.26*	11.36	7.89**
Shova×SS	14.01**	-12.22**	17.14**	7.67	-11.78**	-5.73**	28.27**	18.79	10.72**
Shova×Arka Kirti	7.26**	-7.39**	18.44**	22.30**	-13.33**	-3.68**	35.76**	17.27	10.88**
Shova×Pusa Chitrakshya	14.72**	-11.78**	11.20**	1.06	-14.90**	-1.10	30.49**	31.52*	7.17**
Shova×BCKV123	5.08**	-5.99**	8.14**	10.95*	-7.38	-1.55	24.09**	21.21	4.95**
Shova×UHFS 68	6.67**	2.20	7.14**	17.53**	-10.11**	-2.07	19.43**	14.55	6.31**
Shova× UHFS56	16.94**	-3.19*	3.77	14.82**	-4.45	0.97	2.59	9.09	4.60**
ACC-1×SS	17.14**	0.66	14.83**	23.09**	-4.67	-6.51**	14.83*	11.06	7.93**
ACC-1×Arka Kirti	9.92**	0.58	16.67**	26.78**	-9.06*	-5.04**	28.62**	28.03*	9.35**
ACC-1×Pusa Chitrakshya	13.49**	0.69	9.40**	22.84**	-5.74	-4.05**	26.11**	28.33*	6.73**
ACC-1×BCKV123	8.69**	-3.54**	10.64**	23.64**	-5.43	-3.33**	17.56*	20.00	5.32**
ACC-1×UHFS68	1.63	17.69**	7.59**	24.51**	-2.72	-4.72**	29.13**	24.09*	6.49**
ACC-1×UHFS56	12.38 **	8.73**	12.16**	21.47**	-4.39	-5.74**	12.28	22.73	6.41**
SS×Arka Kirti	18.25 **	8.29**	18.26**	33.07**	-10.92**	-6.81**	-11.19	-4.55	11.51**
SS×Pusa Chitrakshya	26.35 **	15.49**	11.76**	27.74**	-11.85**	-4.44**	2.59	-18.18	8.08**
SS×BCKV123	15.56 **	25.30 **	7.67**	28.98**	-9.33*	-3.51**	16.37*	-31.82**	6.13**
SS×UHFS68	21.75 **	1.32	8.55**	19.36**	-11.11**	-4.49**	21.38**	-27.27*	6.29**
SS×UHFS56	14.09 **	3.30 **	3.18	24.65**	-17.78**	-6.87**	17.13*	-13.64	5.04**
Arka Kirti×Pusa Chitrakshya	16.87 **	13.76 **	8.71**	29.95**	-9.68*	-2.76*	36.61**	13.64	6.71**
Arka Kirti ×BCKV123	8.57**	-3.54**	10.00**	33.22**	-9.57*	-4.05**	19.43**	27.27*	7.05**
Arka Kirti ×UHFS68	9.44**	7.85**	10.72**	29.86**	-13.63**	-0.81	2.59	25.00*	6.66**
Arka Kirti ×UHFS56	9.84**	12.91**	9.19**	20.39**	-9.45*	-2.67*	1.05	29.24*	6.13**
Pusa Chitrakshya×BCKV123	13.36**	0.03	7.59**	13.50**	-6.51	-1.19	28.62**	23.48	5.40**
Pusa Chitrakshya ×UHFS68	24.60**	12.72**	8.39**	17.97**	-3.49	-1.09	16.83*	12.42	6.74**
Pusa Chitrakshya ×UHFS56	22.74**	5.33**	4.06	27.77**	-7.91*	-1.53	28.67**	6.82	5.04**
BCKV 123×UHFS68	17.46**	25.27**	13.05**	18.99**	0.43	0.04	25.04**	-5.30	7.83**
BCKV 123×UHFS56	15.67**	16.97**	10.08**	20.00**	2.47	6.36**	8.20	-18.18	5.12**
UHFS68×UHFS56	11.83**	13.76**	9.44**	22.88**	0.56	6.02**	10.24	-13.64	5.76**
SE	**0.79**	**0.15**	**0.55**	**0.93**	**1.53**	**0.92**	**1.42**	**0.26**	**0.70**

significant positive heterosis for the character number of leaves per stem. Heterosis for better parent ranged from (2.57 to 23.83. The range of standard heterosis over check BCKV 123 was recorded in the range (7.59 to 18.44) where the maximum and minimum heterosis was found in (Shova × Arka Kirti) and (Pusa Chitrakshya × BCKV-123) respectively.

The character stalk length exhibited positive significant heterosis (RH) in sixteen hybrids ranging from 8.47 to 16.94. The positive heterosis is desirable for the character stalk length in spray *Chrysanthemum*. Maximum heterosis for flower stalk length in marigold whereas significant negative heterosis was found for the trait number of leaves per stem (20).

Thirteen hybrids were recorded to have significant positive heterosis (RH) for floral attribute number of flower buds per plant, while four hybrids were found to exhibit significant positive heterosis for number of flowers per branch. Seven hybrids were found superior to the standard check for number of flowers per branch and thirteen hybrids were recorded to have significant positive heterosis over the standard check (Table 4). For number of flowers per plant, one hybrid (Shova × ACC-1) was found superior to the better parent and all the hybrids showed superiority to the standard check. High additive gene action is important for flower yield and number of flowers per plant (21, 22). Highly significant GCA values for flower yield reveal the relative importance of additive gene action over non-additive effects (23). The hybrid plants have the highest variability, making them the most suitable for future improvement programs (24).

Significant differences in all traits and a wide variation in progenies were reported for all traits among the gladiolus genotypes in F1 seed (19). Diallel analysis provide the greatly influencing genetic information for breeding programs (25). The flower yield per plant is a valuable trait in heterosis breeding as it directly impacts the potential seed production, overall productivity and success of hybridization. Positive heterosis is desirable for the character flower yield (26, 27). The difference in heterosis for distinct features and negative heterosis observed in some crossings for diverse traits may be attributable to the combination of undesirable genes from their parents (28).

Conclusion

This study confirms the presence of significant heterosis in F1 hybrids of *Chrysanthemum*, particularly for yield-attributing traits such as number of flowers per plant, number of branches per plant and significant negative heterosis for the traits plant height, days to flower bud initiation and days to final bloom. The results provide valuable insights for breeders aiming to develop new *Chrysanthemum* varieties with enhanced ornamental value. Among all the hybrids SS × Arka Kirti Shova× Arka Kirti, BCKV 123 ×UHFS-56 showed highest yield attributes. In the current study, the estimates of heterosis, when compared to the mid-parent, better parent, or standard check, showed significant variability in both directions among the hybrids for all the traits examined. The results may vary as per different growing conditions. This is because factors contribute to different results in different locations. These parameters need to be considered when interpreting the results because they significantly affect the performance of the plants.

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Authors' contributions

DK, MRN carried out the sequence alignment and drafted the manuscript. BPS, SKP and SB participated in the sequence alignment. KKP, GN participated in the design of the study and performed the statistical analysis. KM and SS participated in its design and coordination. All authors read and approved the final manuscript.

Compliance with ethical standards

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