

Original research

Significance of floral axis and staminal features in tracing phylogeny of *Cleome* species

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Abstract

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Taxonomic delimitation, phylogeny of *Cleome* L. species and relative closeness between three allied families, Capparaceae, Cleomaceae and Brassicaceae, are enigmatic and yet to be resolved comprehensively. The genus *Cleome* of Cleomaceae represents a cosmopolitan assemblage of species with wide variability in morphological features sharing morphological similarity with both Capparaceae and Brassicaceae. In the present study, floral-axis and staminal features, along with habit and leaf characters, were employed in tracing the phylogeny of *Cleome* species not explored earlier. The parameters proved unique in solving the phylogenetic puzzle of *Cleome*, allowing to speculate on the origin of woody and non-woody herbaceous species of *Cleome* from two separate species aggregates of Capparaceae (palmate-leaved *Crateva* aggregate and simple-leaved *Capparis* aggregate, respectively), also to establish phylogenetic linkage between three families, Capparaceae, Cleomaceae and Brassicaceae. Evolutionary changes were directed towards the gradual shortening and suppression of elongated floral axis to discoid thalamus, gradual reduction in the number and size of stamens, and flower size with habitual transformations from shrubby to herbaceous form. *Cleome* appeared as a connecting link between Capparaceae and Brassicaceae, and the interpretations derived showed significant concomitance with APG IV classification system.

Keywords: Brassicaceae, Capparaceae, *Cleome*, evolutionary trends, morphology, reproductive features.

INTRODUCTION

Cleome L. is the largest genus of the family Cleomaceae, comprising 180 to 200 species of herbaceous annual or perennial plants widely distributed throughout the tropical and subtropical regions of the globe (Abdullah et al., 2016). Earlier, Cleomaceae was treated as a subfamily of Capparaceae but later elevated to the rank of a family as had been proposed by previous taxonomists (Airy Shaw, 1965; Hutchinson, 1967).

The relative closeness of three families, Capparaceae, Cleomaceae and Brassicaceae, is a matter of

great debate, yet to be resolved conclusively. Phylogeny derived from morphological and molecular data recognised three primary clades as families: Capparaceae, Cleomaceae and Brassicaceae (Hutchinson, 1967; Hall et al., 2002; Su et al., 2012). More recently, molecular data from chloroplast genome analysis supported the opinion that Cleomaceae is a monophyletic family, sister to Brassicaceae and two families together form a sister clade to Capparaceae (Alzahrani et al., 2021). Cleomaceae is considered one of the closest relatives of the family Brassicaceae, also known as the “sister of Crucifers”, but with a much wider range of floral morphology (Bayat et

al., 2018). In APG IV (2016) classification, all three closely related families are included under the order Brassicales.

Some of the previous studies on Cleomaceae have involved floral morphology and development (Patchell et al., 2011), the evolution of C4 photosynthesis (Feodorova et al., 2010; Mabry et al., 2020; Walden et al., 2020; Hoang et al., 2023), pollination biology (Cane, 2008). Phylogeny of Cleomaceae was reconstructed using data from three genomes comprising three *cpDNA*, one *mtDNA* and one *nrDNA* (ITS) that supported the monophyly of 14 out of 15 clades identified previously (Patchell et al., 2014). Morphological parameters often have played a significant role in tracing phylogenetic linkage. Leaf types, the transition from zygomorphy to actinomorphy (Endress, 1999; Cubas, 2004), decreasing number of stamens (Mitchell & Diggle, 2005), and fruit types (Xiang et al., 2017) have been proven very effective in establishing phylogenetic linkage between species. The nature and character of the floral axis or thalamus and staminal features can be informative and unique in establishing phylogeny.

In the present investigation, an evolutionary trend was outlined between Capparaceae and Brassicaceae, considering *Cleome* of Cleomaceae a connecting link between two families, based primarily on the morphology of the floral axis, staminal characters, and habits. Two evolutionary sequences leading to the origin of different *Cleome* species were also predicted. The present work aimed to highlight an assumption that the elongated floral axis (differentiated into androphore and gynophore and its gradual shortening into discoid thalamus) can play a vital role in establishing phylogenetic relationships between different *Cleome* species, as well as between three allied families, Capparaceae, Cleomaceae and Brassicaceae. Gradual shortening and suppression of elongated floral axis may be the direction of evolutionary advancement.

MATERIALS AND METHODS

Nine species of *Cleome* comprising both woody and non-woody herbaceous members (*Cleome gynandra* L., *Cleome speciosa* Raf., *Cleome spinosa*

Table 1. The studied *Cleome* species, time of studies and vouchers of studied specimens

Species	Time of studies	Voucher specimen
<i>Cleome gynandra</i>	July–September	1. West Bengal, CNH, BSI, No. 30403
		2. West Bengal, CNH, BSI, No. 256
		3. Andhra Pradesh, CNH, BSI, No. 9676
		4. Tamil Nadu, CNH, BSI, No. 84463
<i>Cleome speciosa</i>	April–May	1. West Bengal, CNH, BSI, No. 59172
<i>Cleome spinosa</i>	April–September	1. Philippines, CNH, BSI, No. 28179
<i>Cleome viscosa</i>	March–July	1. West Bengal, CNH, BSI, No. 41
		2. West Bengal, CNH, BSI, No. 44
		3. West Bengal, CNH, BSI, No. 79253
		4. Tamil Nadu, CNH, BSI, No. 60831
<i>Cleome rutidosperma</i>	May–November	1. West Bengal, CNH, BSI, No. 10846
		2. West Bengal, CNH, BSI, No. 44608
<i>Cleome monophylla</i>	June–November	1. West Bengal, CNH, BSI, No. 9832
		2. Maharashtra, CNH, BSI, No. 563869
		3. Madhya Pradesh, CNH, BSI, No. 14412
		4. Chennai (TN), South India, CNH, BSI, No. 18680
		5. Orissa, CNH, BSI, No. 20516
<i>Cleome simplicifolia</i>	July–August	1. Maharashtra, CNH, BSI, No. 39534
		2. Gujrat, CNH, BSI, No. 63821
		3. Uttar Pradesh, CNH, BSI, No. 5619
<i>Cleome scaposa</i>	August–December	1. Rajasthan, CNH, BSI, No. 2680
		2. Rajasthan, CNH, BSI, No. 642
<i>Cleome aspera</i>	May–July	1. Kerala, CNH, BSI, No. 65017
		2. Tamil Nadu, CNH, BSI, No. 2218

sa Jacq., *Cleome viscosa* L., *Cleome rutidosperma* DC., *Cleome monophylla* L., *Cleome simplicifolia* Hook. f. & Thomson, *Cleome scaposa* DC. and *Cleome aspera* J. Koenig ex DC.) were studied morphometrically.

Several field visits were conducted from May to December in 2021–2022. Plants were collected, determined in the field, and later dried, and herbarium sheets were prepared. Most of the studied species (*Cleome gynandra*, *Cleome viscosa*, *Cleome spinosa*, *Cleome speciosa*, *Cleome rutidosperma*, *Cleome monophylla* and *Cleome aspera*) were collected in West Bengal as weeds in waste places. Two species (*Cleome scaposa* and *Cleome simplicifolia*) were collected in Southern and Western India, growing on arid, sandy soil. The plant specimens were collected chiefly from different locales of West Bengal and a few from adjoining states (Table 1). The taxonomic identity of the herbarium samples was authenticated by studying the voucher specimens preserved at Central National Herbarium (hereafter referred CNH; acronym CAL) of the Botanical Survey of India (hereafter referred BSI), Shibpur, Howrah, West Bengal, India.

Flowers were dissected using a simple dissecting microscope and characterised morphologically. Nine morphological characters (Table 2), mainly qualitative and quantitative reproductive traits, were taken into consideration (habit, andromonoecy, leaf type, presence or absence of androphore and gynophore, length of gynophore, diameter of flower, number of stamens and ratio of stamen and petal length). Character states were identified (Table 2). The distribution of character states in different species was tabulated in a similarity matrix, assigning character states under each character with a definite number. Two quantitative characters (diameter of flower and length of gynophore) were measured. Ten specimens for each species were studied and characterised. In the case of quantitative estimation, an average of ten observations were taken for each specimen.

The similarity between different species pairs was estimated regarding pairing affinity values. Pairing affinity values (i.e. similarity between a pair of species) were calculated by subtracting the total number of similar character states in species A and B by the total number of character states in species A and B and multiplying by 100. A dendrogram showing a similarity-based clustering pattern was computed

Table 2. Analysed characters of *Cleome* species and their states

No.	Character	Character state
1.	Habit	
	Woody	1
	Herbaceous	2
2.	Andromonoecy	
	Present	1
	Absent	2
3.	Leaves	
	Simple	1
	Compound, trifoliolate	2
	Simple and trifoliolate	3
	Compound, 3–5-foliolate	4
4.	Diameter of flower	
	Less than 1.0 cm	1
	1.0–2.0 cm	2
	More than 2.0 cm	3
5.	Androphore	
	Present	1
	Absent	2
6.	Gynophore	
	Present	1
	Absent	2
7.	Length of gynophore	
	Up to 1.0 cm	1
	1.0–3.0 cm	2
8.	Ratio of stamen and petal length	
	Stamen shorter than or equal to petal	1
	Stamen longer than petals	2
9.	Number of stamens	
	Stamens six	1
	Stamens more than six	2

from pairing affinity values by applying the complete linkage method using the statistical software *MINITAB 19*.

RESULTS

Morphological characterisation and grouping of *Cleome* species

The species of *Cleome* under study were evaluated mainly by their reproductive characters. Nine qualitative and quantitative characters with character states were considered. Still, emphasis was given to features like the structure of the floral axis, presence or absence of androphore or gynophore and their

length, size of the flower, number and nature of stamens, habit and leaf characters. The similarity matrix (Table 3) reflected the character-wise similarity among the studied species.

Among the species studied, *Cleome monophylla*, *Cleome simplicifolia* and *Cleome scaposa* were simple-leaved, while others, except *Cleome aspera*, showed palmately compound leaves. *Cleome aspera* appeared as an intermediate form, having lower 3-foliate compound leaves and upper simple leaves. Most of the species had a constant number (six) of stamens, except *Cleome viscosa* and *Cleome simplicifolia*, which had more than six. Andromonoecy is a unique feature shown by *Cleome gynandra* (Table 3).

Variability among the species in terms of two quantitative characters, i.e. flower diameter and gynophore length, reflects the relative closeness among the species (Table 4). *Cleome gynandra* and *Cleome speciosa* exhibited much extended floral axis with both androphore and gynophore, most extended in *Cleome speciosa* followed by *Cleome gynandra*. The length of androphore in both species was 1.0–1.2 cm. Species like *Cleome spinosa*, *Cleome rutidosperma*, *Cleome monophylla* and *Cleome aspera* showed much shorter floral axis with gynophores only having varying lengths, while in *Cleome viscosa*, *Cleome simplicifolia* and *Cleome scaposa* floral axis was suppressed to a discoid thalamus. *Cleome spe-*

Table 3. States of the analysed characters of *Cleome* species: *Cleome gynandra* (A), *Cleome speciosa* (B), *Cleome spinosa* (C), *Cleome viscosa* (D), *Cleome rutidosperma* (E), *Cleome monophylla* (F), *Cleome simplicifolia* (G), *Cleome scaposa* (H) and *Cleome aspera* (I)

No.	Characters with character states	Character states by species								
		A	B	C	D	E	F	G	H	I
1.	Habit	1	1	1	1	2	2	2	2	2
2.	Andromonoecy	1	2	2	2	2	2	2	2	2
3.	Leaves	4	4	5	4	2	1	1	1	3
4.	Diameter of flower	3	3	3	2	2	2	1	1	1
5.	Androphore	1	1	2	2	2	2	2	2	2
6.	Gynophore	1	1	1	2	1	1	2	2	1
7.	Length of gynophore	2	3	2	-	1	1	-	-	1
8.	Ratio of stamen and petal length	2	2	2	1	1	1	1	1	1
9.	Number of stamens	1	1	1	2	1	1	2	1	1

Table 4. Flower diameter and length of gynophore of the studied *Cleome* species. Mean and standard errors are presented in the upper row; minimum and maximum values are shown in the lower row

Species	Diameter of flower (cm)	Length of gynophore (mm)
<i>Cleome gynandra</i>	2.49 ± 0.020	26.86 ± 0.331
	2.2–2.7	22–30
<i>Cleome speciosa</i>	2.70 ± 0.017	46.93 ± 0.650
	2.5–2.8	38–50
<i>Cleome spinosa</i>	2.36 ± 0.024	22.06 ± 0.457
	2.2–2.7	18–26
<i>Cleome viscosa</i>	1.86 ± 0.021	Gynophore absent
	1.6–2.0	
<i>Cleome rutidosperma</i>	1.87 ± 0.021	1.72 ± 0.029
	1.7–2.0	1.5–2.0
<i>Cleome monophylla</i>	1.77 ± 0.022	0.83 ± 0.016
	1.5–2.0	0.7–1.0
<i>Cleome simplicifolia</i>	0.87 ± 0.015	Gynophore absent
	0.7–1.0	
<i>Cleome scaposa</i>	0.81 ± 0.013	Gynophore absent
	0.6–0.9	
<i>Cleome aspera</i>	0.51 ± 0.014	0.82 ± 0.014
	0.4–0.7	0.7–1.0

ciosa showed the largest flower and the longest gynophore, followed by *Cleome gynandra* and *Cleome spinosa*. Gynophore length in *Cleome monophylla* and *Cleome aspera* was almost the same, though the flowers were much smaller in *Cleome aspera* than *Cleome monophylla*. *Cleome rutidosperma* was similar to *Cleome monophylla* and *Cleome aspera* by gynophore length. Still, it appeared much closer to *Cleome aspera* in leaf morphology, as *Cleome aspera* showed lower trifoliate leaves like *Cleome rutidosperma* along with upper simple leaves.

The relative closeness between the species was assessed regarding pairing affinity values (Table 5). The highest pairing affinity value (77.77%) was shown by three species pairs: *Cleome gynandra* and *Cleome speciosa*, *Cleome rutidosperma* and *Cleome aspera*, *Cleome monophylla* and *Cleome aspera*. The lowest pairing affinity value (11.76%) was shown by two species pairs: *Cleome gynandra* and *Cleome scaposa*, *Cleome speciosa* and *Cleome simplicifolia*. Two species, *Cleome gynandra* and *Cleome simplicifolia*, were utterly different from each other, showing no similarity at all.

Dendrogram (Fig. 1) computed from pairing affinity values showed two clear species groupings; palmate-leaved and simple-leaved species were grouped separately. Palmate-leaved *Cleome gynandra*, *Cleome speciosa* and *Cleome spinosa* were grouped in group A, characterised by woody annual or biennial habit, palmately compound 3–7-foliolate leaves, with androphore and (or) gynophore, a fixed number (6) of exerted stamens, whereas group B comprised six species, *Cleome aspera*, *Cleome scaposa*, *Cleome simplicifolia*, *Cleome monophylla*, *Cleome rutidosperma* and *Cleome viscosa*, characterised by

a woody or non-woody herbaceous habit, 3–5-foliolate to simple leaves, with or without gynophore. The four simple-leaved species (*Cleome monophylla*, *Cleome aspera*, *Cleome simplicifolia* and *Cleome scaposa*) formed the core assemblage in group B and 3–5-foliolate compound-leaved *Cleome rutidosperma* and *Cleome viscosa* appeared allied with simple-leaved species.

DISCUSSION

Variation in habits, floral and fruit forms, attributed to the designation of Capparaceae as a “trash-basket” family comprising many unrelated plants. Based on morphological and molecular data analysis, phylogeny distinguished two subfamilies under Capparaceae, i.e. Capparaceae subfam. Cleomoideae and Capparaceae subfam. Capparoidae, and revealed Cleomoideae as sister to Brassicaceae, not to Capparoidae, making Capparaceae a paraphyletic lineage

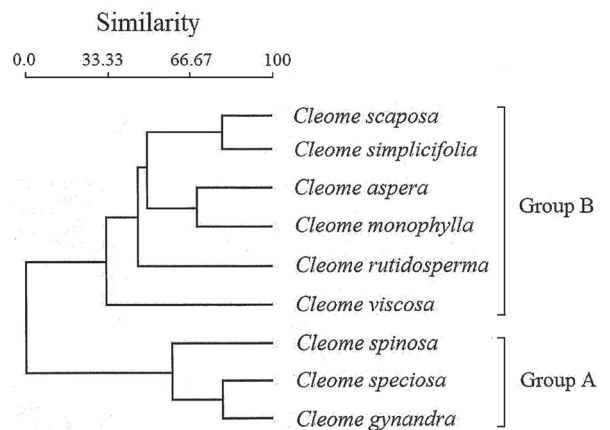


Fig. 1. Dendrogram computed from pairing affinity values on morphology showing the grouping of *Cleome* species

Table 5. Pairing affinity values on morphological and reproductive character states. Species: A – *Cleome gynandra*, B – *Cleome speciosa*, C – *Cleome spinosa*, D – *Cleome viscosa*, E – *Cleome rutidosperma*, F – *Cleome monophylla*, G – *Cleome simplicifolia*, H – *Cleome scaposa*, I – *Cleome aspera*

Species	A	B	C	D	E	F	G	H	I
A	100								
B	77.77	100							
C	66.66	66.66	100						
D	23.52	35.29	35.29	100					
E	22.22	33.33	44.44	47.05	100				
F	22.22	33.33	44.44	47.05	44.44	100			
G	00.00	11.76	23.52	62.50	47.05	58.82	100		
H	11.76	23.52	35.29	50.00	58.82	70.58	87.50	100	
I	22.22	33.33	44.44	35.29	77.77	77.77	58.82	70.58	100

and recognising three primary clades as families, Capparaceae, Cleomaceae, and Brassicaceae (Hutchinson, 1967; Hall et al., 2002; Su et al., 2012).

Role of reproductive structures in tracing phylogeny in Cleomaceae, Capparaceae and Brassicaceae

Gradual transformation in reproductive structures can be a good indicator of evolutionary trends, i.e. a gradual decrease in the number and size of stamens, size of flower, the transition from free stamens to stamens with adhesion or cohesion, from flower actinomorphy to zygomorphy, from polypetalous to gamopetalous condition, from bisexual to unisexual condition and from monoecious to the dioecious stage. In some flowers, the axis nature of the thalamus is quite prominent, showing differentiation into distinct nodes and internodes. The internodes between the calyx and corolla, corolla and androecium and androecium and gynoecium are known as anthophore, androphore and gynophore, respectively. The elongated floral axis with androphore and gynophore represents the primitive condition in Capparaceae. It can be presumed that gradual shortening and suppression of the elongated floral axis have resulted in the formation of short discoid thalamus, where floral leaves arise from highly suppressed nodes. Flowers with elongated unequal exerted stamens represent the comparatively primitive condition, while flowers with fewer included stamens with uniform patterns represent a derived condition. Though the first recorded angiosperm leaves were simple and entire, favouring the concept that compound leaves might have reappeared independently through different lineages several times in other taxa, few of which might have evolved back to simple leaves (Taylor & Hickey, 1996; Doyle & Endress, 2000; Bharathan et al., 2002).

Studies on molecular parameters and a few overlapping morphological features have convincingly established relative closeness between Cleomaceae, Capparaceae and Brassicaceae. The present study outlines the probable routes of evolution of different *Cleome* species from various Capparaceae members. The members of Capparaceae are generally distinguishable from those of Cleomaceae and Brassicaceae by plesiomorphic features like woody

shrubby habit, many free-exserted stamens and fleshy indehiscent fruits without replum. The closer affinity between Cleomaceae and Brassicaceae is evidenced by herbaceous habit, replum in the dehiscent siliqua-type fruit, and a reduced number of stamens. The primary leaf pattern in three families, Capparaceae, Cleomaceae and Brassicaceae, shows plasticity. Stamen number is highly variable in Capparaceae, which indicates a definite direction of evolution from *Capparis* (with a large number of stamens) to Cleomaceae and Brassicaceae (having a fixed number of six stamens) (Erber & Leins, 1997a, 1997b). Fleshy, indehiscent fruit is a plesiomorphic feature in Capparaceae and Brassicaceae, a dominant fruit type in Capparaceae. At the same time, Brassicaceae and Cleomaceae share a synapomorphy having dehiscent siliqua-type fruit with replum (Judd et al., 1994, 1999).

Evolutionary trends in *Cleome* species

The genus *Cleome* represents a cosmopolitan assemblage of species with a wide range of morphological variability like - simple to palmately compound leaves, woody herbaceous to small procumbent or decumbent herbaceous habit, differentiation of floral axis into both androphore and gynophore or only gynophore or reduced to flattened thalamus, varying number of free stamens, siliqua-type of dehiscent fruit, showing resemblance with both Capparaceae and Brassicaceae. Such variability indicates the multiple origins of different *Cleome* species. The *Cleome* species might have originated from two species aggregates of Capparaceae: palmate-leaved *Crateva* aggregate (*Crateva nurvala*, *Crateva unilocularis*, *Crateva tapia*, *Crateva religiosa*) and simple-leaved *Capparis* aggregates (*Capparis spinosa*, *Capparis roxburghi*, *Capparis cinerea*, *Capparis cantoniensis*, *Capparis assamica*). The members of *Crateva* aggregates are characterised by a zygomorphic flower, the extended floral axis with both androphore and gynophore, a variable number of stamens, and an indehiscent berry type of fruit. Those simple-leaved *Capparis* aggregates are characterised by a zygomorphic flower, many free stamens, the presence of gynophore only, and an indehiscent berry type of fruit. The woody, herbaceous species of *Cleome* (*Cleome speciosa*, *Cleome gynandra* and *Cleome spinosa*)

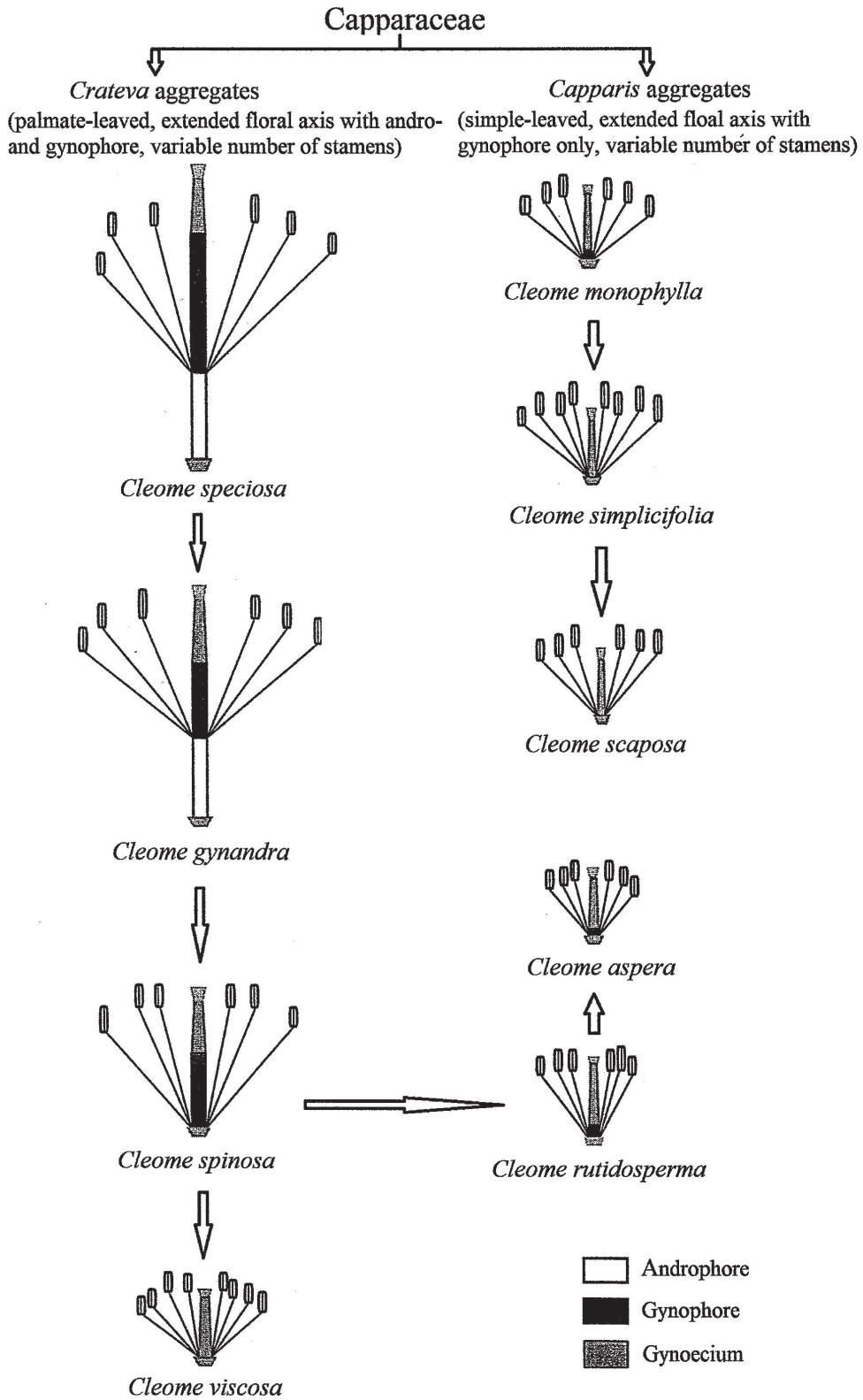


Fig. 2. Diagrammatic illustrations of probable evolutionary changes in the floral axis leading to the origin of different *Cleome* species from palmate-leaved and simple-leaved *Crateva* aggregate and *Capparis* aggregate, respectively

with palmately compound 3–7-foliolate leaves, androphore and (or) gynophore, zygomorphic flower, a limited number of stamens, dehiscent siliqua-type fruit might have originated from the *Crateva* aggregates. *Cleome speciosa* (with both androphore and long gynophore of 3.8–5.0 cm) appeared as the immediate descendent followed by *Cleome gynandra* (with androphore and smaller gynophore of 2.2–3.0 cm), *Cleome spinosa* (without androphore with gynophore only of 1.8–2.6 cm) and *Cleome viscosa* (without both androphore and gynophore) (Fig. 2). Small, herbaceous, non-woody, erect, procumbent or decumbent species of *Cleome* (*Cleome simplicifolia*, *Cleome scaposa*, and *Cleome monophylla*) with simple leaf, limited number of stamens, with or without small gynophore, dehiscent siliqua-type fruit might have evolved from the *Capparis* aggregates. *Cleome monophylla* (with small gynophore and six stamens) appears to be the immediate descendent, followed by *Cleome simplicifolia* (without gynophore but with more than six stamens) and *Cleome scaposa* (without gynophore and with six stamens). *Cleome aspera*, a descendant from *Cleome rutidosperma*, appeared as the intermediate form between the two phyletic lines in having lower compound trifoliolate leaves and upper simple leaves (Fig. 2). The doctrine of character correlation between the decrease in floral axis length and stamen numbers was not found to be followed in case of *Cleome simplicifolia*. Evolution does not need to involve all organs of a plant at the same time; one organ may be advancing while the other is stationary or reverting.

In both the phyletic lines, the evolutionary changes are presumed to have directed towards habitual shifting from woody erect herbaceous to erect, decumbent or procumbent non-woody herbaceous condition, gradual shortening or suppression of floral axis and decrease in size of flower and number of stamens ultimately leading to small *Cleome* species with small flowers, fixed six stamen condition, suppressed discoid thalamus, and siliqua-type of fruit through convergent evolution.

The grouping of taxa in the dendrogram (Fig. 1) strongly supported the origin of *Cleome* species following two separate evolutionary trends. In the dendrogram, *Cleome speciosa* showed a much closer affinity with *Cleome gynandra* than *Cleome spinosa* and a much distant relationship with *Cleome viscosa*

and *Cleome rutidosperma*. Supporting the predicted evolutionary trend from *Capparis* aggregates, all simple-leaved forms with or without gynophore were included in a core group with a significantly high similarity level. *Cleome viscosa*, though broadly included in group B, appeared to be a connecting link between two groups, characterised by 3–5-foliolate palmate leaves, small flowers, and a limited number of inserted stamens (8–12) with staminodes, absence of gynophore. The presence of non-functional staminodes is often considered an intermediate phase in reducing stamen number (Walker-Larsen & Harder, 2000).

Origin of Brassicaceae members from *Cleome*

Members of Brassicaceae are presumed to have differentiated from or shared a common ancestor with Cleomoideae (Cleomaceae) linked through tentative basal members of Brassicaceae tribe Stanleyeae (Takhtajan, 1980). Phylogenetic analysis using morphological and molecular data indicated that *Cleome* is more closely related to Brassicaceae than *Capparis* (Judd et al., 1994; Rodman et al., 1998). Species of *Cleome*, as well as its probable progenitors, are characterised by zygomorphic flowers. Almost all Brassicaceae members are actinomorphic, though zygomorphy is found in 10 genera (Endress, 1992). The presence of gynophore, lack of tetradynamous stamen, and woody habit in a few presumed basal members of Brassicaceae consolidate the ancestral status of the Capparaceae subf. Cleomoideae for Brassicaceae (Conquest, 1981; Rollins, 1993).

CONCLUSIONS

Interpretations derived in the present study showed strong concomitance to those derived from molecular data and APG IV classification. *Cleome* appeared as a connecting link between Capparaceae and Brassicaceae. The nature of the floral axis, staminal features and habit proved to be unique parameters in solving disputes over phylogenetic relationships between three families: Capparaceae, Cleomaceae and Brassicaceae. Future studies involving more *Cleome* species must address the continuity in the evolutionary sequences with adequate perfection and project an improved version of this interpretation.

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