Taxonomy and Biosystematics

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Abstract

Momordica belongs to the subtribe Thalidianthinae Pax, tribe Joliffieae Schrad., subfamily Cucurbitoideae of Cucurbitaceae. Chakravarty (1959) enumerated seven species from India. De Wilde and Duyfjes (Bot Z 87:132–148, 2002) list out ten species from Asia of which six each occur in India and Malaysia. Joseph and Antony (Indian J Plant Genet Resour 23:172–184, 2010) presented a taxonomic revision of the genus for India. They recognized six species: *M. balsamina* L., *M. charantia* L., *M. dioica* Roxb., *M. sahyadrica* Joseph and Antony, *M. subangulata* Blume [subsp. *renigera* (G. Don) W. J. de Wilde] and *M. cochinchinensis* (Lour.) Spreng. *M. dioica* sensu stricto comprises delicate forms with evening anthesis and intensely musky scented flowers, distributed in low elevation areas in the Western Ghats, and in peninsular and Central India. Stout forms with day anthesis and large showy flowers occurring in mid and high elevation Western Ghats are separated as a new species (*M. sahyadrica* Joseph and Antony). North-eastern elements, presently treated under *M. dioica*, are placed under *M. subangulata* ssp. *renigera*. *M. macrophylla* Gage has been placed in synonymy with *M. cochinchinensis*. The presence of *M. denudata* (Thwaites) C. B. Clarke in India is doubtful in the absence of valid herbarium specimens or field collections from the reported localities. Generic and specific descriptions, key to species, and notes on distribution, habitat and ecology are also provided. A biosystematic account of the genus for the Indian taxa comprises morphology, molecular taxonomy, cytology, crossability and conclusions on evolutionary relationship are also presented.

Keywords

Momordica · Systematics · Taxonomic key · Evolutionary relationship · Seed fat

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Taxonomy

Momordica belongs to the subtribe Thalidianthinae Pax, tribe Joliffieae Schrad., subfamily Cucurbitoideae of Cucurbitaceae (Jeffrey 1980; de Wilde and Duyfjes 2002). Generic and species descriptions (along with keys in some cases) are found in various monographic and floristic treatises (Willdenow 1805; Blume 1826; Seringe 1828; Wight and Arnot 1841; Thwaites 1864; Hooker 1871; Clarke 1879; Keraudren 1975; Jeffrey 1980). No comprehensive monographs covering taxonomy and nomenclature of *Momordica* species are known to exist.

The similarity of the common characters, taken as key to distinguish between dioecious taxa of *Momordica* has led to widely conflicting taxonomic treatments of this genus in South and South–East Asia. An understanding of the taxonomy of the target taxa and their distribution is the basic prerequisite for undertaking a viable conservation programme. It is essential to ascertain a taxon's correct scientific name if a specimen is to be linked to the wealth of information that may be known about the taxon to which it belongs. Misidentification of any material will lead to spurious results when the germplasm is studied and used.

History

The taxonomic treatment of the genus *Momordica* is quite extensive. Generic and species descriptions along with keys are found to be varying in degrees in various floras published in India before 1947. Van Rheede's (1688) descriptions and illustrations of paval (=*Momordica charantia*) in the *Hortus Malabaricus* is the first printed record. Linnaeus (1753), de Candole (1828), Roxburgh (1832), Clarke (1879), Cooke (1901), Gamble and Fischer (1919), Blatter (1919) and Kanjilal et al. (1938) have extensively dealt with the systematics of the genus. After 1947, Santapau (1953), Saldhana and Nicholson (1976), Chakravarty (1959, 1982) and Mathew (1981, 1983) have treated the genus in their floristic works. Many of the regional and district floras also mention and give a small description of various *Momordica* species (Srivastava 1976; Oommachan 1977; Bhandari 1978; Naik 1979; Rao 1985; Shetty and Singh 1987; Ramachandran and Nair 1988; Vajravelu 1990; Narasimhan and Sharma 1991; Deshpandey et al. 1993; Kothary and Murthy 1993; Chauhan 1996; Sasidharan and Sivarajan 1996; Sivarajan and Mathew 1997; Pallithanam 2001; Singh et al. 2002; Bhat 2003).

Chakravarty's (1982) treatment of *Momordica* in his *Fascicles of Cucurbitaceae* is the classification that is by far the most relied upon in India. He has enumerated seven species from India including *M. denudata* from Kerala and *M. macrophylla* from the Assam–Manipur belt bordering Myanmar. Gamble and Fischer (1919) mention occurrence of *M. denudata* in Kerala from "low country Quilon", which might have prompted Chakravarty (1982) to mention its distribution in Kerala. He has also described a new variety, i.e. *M. charantia* var. *muricata* based on Rheede's plate in *Hortus Malabaricus* as type. Jeffrey (1980) rules out *M. subangulata* from India for the absence of ridged or longitudinally alate fruits and hence treats this component under *M. dioica*. Kumar and Pandey (2002) also worked on the taxonomy and diversity of the genus in India. However, it does not vary substantially from that of Chakravarty (1982) and reports the same number of species and distribution in India. Joseph and Antony (2010) have recently revised the genus for India.

Trimen (1893–1900) gives a detailed technical description and key to the species of *Momordica* occurring in Sri Lanka. Backer and Brink (1963), Henderson (1974), and Keraudren (1975) give detailed floristic account of *Momordica* species in other South–East Asian countries. De Wilde and Duyfjes (2002) give a detailed taxonomic treatment of the genus in south and South–East Asia. They have thoroughly revised the species concept and according to them *M. cochinchinensis* and *M. subangulata* do not occur in South India. A new subspecific rank in *M. subangulata* has been proposed which partially includes material

treated under *M. dioica* of north-eastern India. A considerable part of the taxa hitherto treated under *M. cochinchinensis* has been taken out and placed under *M. denticulata*. This study is of much interest as it covers all Indian species and the Malaysian taxa, which has affinity with the north-eastern, Andaman and Western Ghats taxa. Oliver (1979) gives keys and detailed descriptions of various African species of *Momordica*.

Delimitation of the Taxon

The species falling under *Thalidiantha*, *Cyclanthera*, *Ecbalium*, *Luffa* and *Diplocyclos* were included by different workers under the genus *Momordica*. Chakravarty (1982) retained separate taxon status for *M. macrophylla*, distinct from *M. cochinchinensis* for the unlobed nature of leaves. Heterophylly is observed in *M. dioica* (Bharathi 2010) and *M. sahyadrica* (Joseph 2005). Primary leaves, fully grown leaves and late growth stage leaves of these taxa vary in shape especially in lobing even in tuber sprouts. Hence, leaf shape may not be a reliable character in distinguishing species in the dioecious group. *M. cymbalaria* Fenzl ex Naud. (syn. *M. tuberosa* (Roxb.) Cogn.) was originally described as *Luffa tuberosa* by Roxburgh (1814, 1832) and renamed as *M. cymbalaria* Fenzl. and the name was adopted (Clarke 1879). Cogniaux (1881) placed it under *M. tuberosa* (Roxb.) Cogn., based on Roxburgh's *Luffa tuberosa.* The fruit was like that of *Luffa amara* Wall., but without stopple and with only eight angles (Roxburgh 1832). Absence of stopple which is one of the generic characters of *Luffa* was the reason to transfer this species to the genus *Momordica*. Chakravarty (1959) stated that *Momordica* is characterised by the presence of true cystoliths of Calcium Carbonate on the lower surface of the leaf which are absent in *M. cymbalaria*. Further, based on evidence from breeding behaviour, pollination biology and comparative morphology, Joseph and Antony (2010) place it under *Luffa* in their biosystematic treatment of *Momordica*. Bharathi et al. (2011, 2012a) highlighted its distinctness from other *Momordica* species of Indian occurrence. On the other hand, *M. cymbalaria* is reported to be closer to African species like *M. humilis*, *M. kirkii*, *M. boivinii* and *M. sessilifoilia* (Schaefer and Renner 2010) and *M. cabraei* (Ali et al. 2010).

Diagnostic Characters

Throughout the taxonomic treatments of *Momordica*, certain characters ('general' representing the genera and 'specific' applicable to individual taxa) have repeatedly been used to define and distinguish the genus. The major diagnostic features of the genera are the presence of conspicuous floral bracts (male), calyx cup, entire petal, scales on corolla, pendulous, echinate or muricate fruits, sculptured seeds and viny habit. Within the genus, three subgeneric groups can be recognised based on sex expression and habit (Table 4.1). Once these major divisions have been made, several other characters are used to distinguish within the subgenera. These minor diagnostic characters are flower colour, petal shape and size, petal markings, pubescence, bract shape, position, calyx cup colour, sepal shape, gland dottedness (petiole), floral scent, anthesis time, seed sculpture, shape, colour, pollinators, fruit surface ornamentation, etc.

Current Taxonomic Status

As different workers have treated it differently, there is no clarity and consensus in the interspecific taxonomy of the genus *Momordica* L. Taxonomic confusion exists because of the widespread use of common names. The botanical names and common names are used incorrectly or interchangeably and are often misleading. For example, *M. subangulata* subsp. *renigera* is referred as *M. cochinchinensis* (Ram et al. 2002; Sanwal et al. 2011) and *M. dioica* (Ali et al. 1991). Similarly, the descriptions of morphological features of many species are incorrect or incomplete, further compounding the problem. A perusal of over 700 sheets lodged

Table 4.1 Subgeneric classification of Indian *Momordica*

SN	Character	Subgenus A	Subgenus B	Subgenus C
1	Basic chromosome number (*n*)	11	14	9
2	Breeding behaviour	Monoecious	Dioecious	Monoecious
3	Germination	Epigeal	Hypogeal	Hypogeal
4	Habit	Annual	Perennial	Perennial
5	Roots (tap root)	Fibrous	Tuberous	Tuberous
6	Fruit surface	Muricate-tubercled	Echinate-soft papillate	Ribbed
7	Seed sides	Rectangular, squarish	Cog wheel, round, oval	Round
8	Male flower bract position	Mid-way or towards axis-not protective	Just below the flower—protective	Absent/ rudimentary
9	Stigma colour	Green	Yellow	Green
10	Leaf shape	Angular	Roundish	Roundish

in major herbaria in India reveals incomplete labelling and misidentification (Joseph 2005). *M. dioica* folders displayed at MH, Coimbatore and CAL (Kolkata) include three distinct entities that vary for many morphological features and represents geographically isolated areas.

Generic characters used to distinguish the genus *Momordica* in most of the earlier works include a calyx tube closed with incurved scales. In fact, instead of the calyx tube it is the corolla which has scales at its base. Similarly, male inflorescence morphology needs explanation as to branched or non-branched nature. Chakravarty (1982) ignored important traits such as anthesis time, petal spot and ridged nature of the fruit. Longitudinally alate or ridged fruits are the key characters for *M. subangulata* (Jeffrey 1980) and blotched petals with black bulls eye patterns that are very specific to *M. subangulata* and *M. cochinchinensis*.

Raj et al. (1993) listed out eight species indigenous to India, namely *M. charantia*, *M. balsamina*, *M. dioica*, *M. cymbalaria*, *M. denudata*, *M. macrophylla*, *M. subangulata* and *M. cochinchinensis*. Of these, *M. macrophylla* is treated as synonymous (Table 4.2) with *M. cohinchinensis* (Jeffrey 1980, 2001; de Wilde and Duyfjes 2002). Joseph and Antony (2010) recently revised the genus for India. Based on an extensive ecogeographic survey in South India including the type of localities, they consider the occurrence/existence of *M. denudata* in India as fairly doubtful (Joseph and Antony 2010). The monoecious taxa are *M. charantia* L. (var. *muricata* (Willd.) Chakrav. and var. *charantia* L.), *M. balsamina* L. and *M. cymbalaria*. The dioecious taxa are *M. dioica* Roxb., *M. sahyadrica* Joseph et. Antony, *M. cochinchinensis* (Lour.) Spreng. and *M. subangulata* Blume subsp. *renigera* (G. Don) W. J. de Wilde.

The taxonomic position of *M. cymbalaria* within the genus *Momordica* had been a matter of considerable debate (Pandey et al. 2006). The two extreme positions are either that *M. cymbalaria* belongs to the genera *Momordica* or *Luffa*. The species *Luffa tuberosa* was established by Roxburgh (1832) and subsequently transferred to the genus *Momordica* as *Momordica cymbalaria* (Clarke 1879). Congiaux (1881) recognised as *Momordica tuberosa* based on Roxburgh's *Luffa tuberosa*. Chakravarty (1959) reported that the leaves of all *Momordica*'s contain true cystoliths on the lower surface which is absent in *M. cymbalaria*. Chakravarty (1982) also mentioned that there is no reason for shift, the species to *Momordica* which has either muricate or echinate fruits but never angular. However, the seed coat anatomy (Singh and Dathan 2001) and seed fat (Azeemoddin and Rao 1967) characteristics supported the retention of this species under the genus *Momordica*. Recently, based on internal transcribed spacer (ITS) sequences of nuclear ribosomal DNA (Ali et al. 2010) and three genome (plastid,

Table 4.2 List of common synonyms of Indian *Momordica* species

SN	IPNI Index	Accepted Nomenclature
1	*Momordica schinzii* Cogn. Ex Schinz (IK)	*Momordica balsamina* Linn.
2	*Momordica garipensis* E. Mey (IK)	*Momordica balsamina* Linn.
3	*Momordica involucrata* E. Mey. (IK)	*Momordica balsamina* Linn.
4	*Momordica cylindrica* Blanco (IK)	*Momordica charantia* Linn.
5	*Momordica muricata* Vell. (IK)	*Momordica charantia* Linn.
6	*Momordica muricata* Wall. (IK)	*Momordica charantia* Linn.
7	*Momordica senegalense* Lam. (IK)	*Momordica charantia* Linn.
8	*Momordica zeylanica* Mill. (IK)	*Momordica charantia* Linn.
9	*Momordica anthelmintica* Schum and Thorn. (IK)	*Momordica charantia* Linn.
10	*Momordica chinensis* Hort. (IK)	*Momordica charantia* Linn.
11	*Momordica elegans* Salisb. (IK)	*Momordica charantia* Linn.
12	*Momordica indica* Linn. (IK)	*Momordica charantia* Linn.
13	*Momordica heyneana* Wall and G. Don (IK)	*Momordica subangulata* Blume. subsp. *renigera* (G. Don) W. J. de Wilde
14	*Momordica renigera* Wall (IK)	*Momordica subangulata* Blume. subsp. *renigera* (G. Don) W. J. de Wilde
15	*Momordica renigera* Wall. and G. Don (IK)	*Momordica subangulata* Blume. subsp. *renigera* (G. Don) W. J. de Wilde
16	*Momordica hispida* Dennst (IK)	*Momordica dioica* Roxb.
17	*Momordica tuberosa* Dennst. (IK)	*Momordica dioica* Roxb.
18	*Momordica wallichii* M. Roem. (IK)	*Momordica dioica* Roxb.
19	*Momordica roxburghiana* G. Don (IK)	*Momordica dioica* Roxb.
20	*Momordica sicyoides* Ser. (IK)	*Momordica dioica* Roxb.
21	*Momordica sicyoides* Sesse and Moc. (IK)	*Momordica dioica* Roxb.
22	*Momordica macrophylla* Gage (IK)	*Momordica cochinchinensis* (Lour.) Spreng.
23	*Momordica mixta* Roxb. (IK)	*Momordica cochinchinensis* (Lour.) Spreng.
24	*Momordica ovata* Cogn. (IK)	*Momordica cochinchinensis* (Lour.) Spreng.
25	*Momordica sphaeroidea* Blanco (IK)	*Momordica cochinchinensis* (Lour.) Spreng.
26	*Momordica suringarii* Cogn. (IK)	*Momordica cochinchinensis* (Lour.) Spreng.
27	*Momordica meloniflora* Hand.-Mazz. (IK)	*Momordica cochinchinensis* (Lour.) Spreng.

Source Compiled from Jeffrey (1980), Chakravarty (1982), Hanelt (2001) and de Wilde and Duyfjes (2002)

mitochondrial and nuclear DNA markers) phylogeny (Schaefer and Renner 2010) the status of this species in *Momordica* is established.

Momordica is monophyletic and the genus can be divided into 11 clades (Schaefer and Renner 2010) that mostly correspond to the morphological clades proposed by Jeffrey and de Wilde (2006). The Asiatic species falls under three sects. Dioecious species like *M. cochinchinensis*, *M. dioica, M. sahyadrica*, *M. denticulata*, *M. denudata*, *M. clarkeana* and *M. subangulata* grouped under the sect. *Cochinchinensis,* and monoecious species *M. charantia* and *M. balsamina* under the sect. *Momordica* and *M. cymbalaria* under the sect. *Raphanocarpus* (Schaefer and Renner 2010).

Taxonomic Key

I. *Germination epigeal*, *annual*, *tap root non-tuberous*, *plants monoecious*, *nectary in male flowers not closed with corolla scales*, *fruits muricate or tubercled*.
   a. Bracts of male flowers about the middle of the flower stalk; fruits small or large,

softly tubercled or muricate with long green ridges; seeds thick, flat on surface, margins edged, thick on sides, broadly rectangular, no distinction between chalazal and micropylar ends, ends subtridentate, heavily or feebly sculptured.
……..…*M. charantia*

b. Bracts of male flowers at the apex of the peduncle, fruits small, distantly soft tubercled, no bumps or ridges; seeds very thin, sides not thick, margins wedged, broadly ovate round with tapering micropylar end, ends roundish, finely pitted and feebly sculptured.
…….. *M. balsamina*

II. *Germination hypogeal*, *perennial*, *tap root tuberous*, *plant dioecious*, *nectary of the male flowers closed with prominent corolla scales*, *fruits echinate*.

a. Petals (3 inner) with black purple blotch, male calyx hypanthium saucer shaped

i. Leaf cordate, unlobed, margins dentate, petiole eglandular, male calyx blackish purple, broad, tip round-oval, fruits faintly ridged, softly echinate, seeds medium sized, rectangularly cog wheel shaped.
……..*M. subangulata* subsp. *renigera*

ii. Leaf unlobed or deeply lobed, margins undulate, petiole gland dotted (6–12 bead like structures, often the lamina base also), male calyx blackish purple, broad, tip triangular, fruits with conical projections, seeds large, penta-hexagonal, subtridentate on ends.
…… *M. cochinchinensis*

b. Petals without purple blotch, male calyx-hypanthium cup shaped.

i. Anthesis in the early morning, flowers large, showy, bright yellow, not scented, male calyx blackish purple, sepals of male flower broad, tip oval, round or scarious.
…….. *M. sahyadrica*

ii. Anthesis in the evening, flowers small, pale yellow, intensely musky scented, male calyx whitish yellow, sepals of male flower narrow acute.
……. *M. dioica*

III. *Germination hypogeal, perennial, tap root tuberous, plant monoecious, male flowers borne in short raceme, anthers asymmetrical, fruits ribbed, arils white, epicarp papery and smooth and seeds shiny, round, non bitten*.
……..*M. cymbalaria*

Biosystematics

Morphology

Morphological studies provide information that can be used for practical plant identification and hypothesising phylogenetic relationships. The limited information available on many important and basic aspects in neglected and underutilised crops hinders their development and sustainable conservation. Besides, the information available about germplasm is scattered and not readily accessible, i.e. found only in regional floras. Pasha and Sen (1989) carried out numerical taxonomic analyses of selected genera of cucurbits, but *Momordica* was represented by *M. charantia* var. *charantia* and *M. charantia* var. *muricata* only. The botanical description of different *Momordica* spp. was not systematic and less information is available in the literature. Comparative morphological features of Indian *Momordica* spp. are presented in Table 4.3 and other south Asian entities in Table 4.4 are based on Chakravarty (1946), de Wilde and Duyfjes (2002), Joseph (2005), Bharathi (2010).

Although both the annual monoecious species (*M. balsamina* and *M. charantia*) share more similarity they can be easily distinguished from each other. The male flower bract is positioned at the base/near the axis or below the middle of the flower stalk in *M. charantia,* whereas in *M. balsamina* it is situated in the upper middle or towards the tip of the peduncle. The anther filaments are fused to give a globose appearance in *M. charantia,* while it is split into lobes in

Table 4.3 Comparative morphology of *Momordica* species of India

Characters	*M. charantia*	*M. balsamina*	*M. dioica*	*M. sahyadrica*	*M. subangulata* subsp. *renigera*	*M. cochinchinensis*	*M. cymbalaria*
Basic chromosome no.	11	11	14	14	14	14	9
Germination	Epigeal	Epigeal	Hypogeal	Hypogeal	Hypogeal	Hypogeal	Hypogeal
Life span	Annual	Annual	Perennial	Perennial	Perennial	Perennial	Perennial
Breeding system	Monoecious	Monoecious	Dioecious	Dioecious	Dioecious	Dioecious	Monoecious
Leaf shape	Angular	Angular	Roundish—triangular	Roundish—triangular	Reniform	Angular	Roundish
Leaf lobing	Lobed	Lobed	Lobed	Lobed	Unlobed	Lobed	Angled
Anthesis	Morning	Morning	Evening	Morning	Morning	Morning	Morning
Reproduction	Sexual	Sexual	Sexual	Sexual	Sexual and vegetative	Sexual	Sexual
Roots (tap root)	Fibrous	Fibrous	Tuberous	Tuberous	Tuberous	Tuberous	Tuberous
Umbilical glands	Absent	Absent	Absent	Absent	Absent	Present	Absent
Production of adventious tubers	Absent	Absent	Absent	Absent	Present	Absent	Absent
Inflorescence type (♂)	Solitary/ pseudoraceme	Solitary/ pseudoraceme	Solitary/ pseudoraceme	Solitary/ pseudoraceme	Solitary/ pseudoraceme	Solitary/ pseudoraceme	Short raceme
Nature of male flower bract	Foliaceous	Foliaceous	Foliaceous	Foliaceous	Foliaceous	Foliaceous	Rudimentary
Flower bract shape (♂)	Flat	Flat	Boat -shaped	Boat -shaped	Hooded	Hooded	Rudimentary
Male flower bract position on stalk	Below middle	Above middle	Tip of the peduncle	Tip of the peduncle	Tip of the peduncle	Tip of the peduncle	Base
Male flower nectary	Closed	Partially closed by corolla scales	Closed by corolla scales	Closed by corolla scales	Closed by corolla scales	Closed by corolla scales	Open from above
Relative size of ♂ and ♀ flowers (corolla)	♂ larger than ♀	♂ larger than ♀	Of equal size	Of equal size	Of equal size	Of equal size	Of equal size
Petal spot	Absent	Absent	Absent	Absent	Present	Present	Absent
Stigma colour	Green	Green	Yellow	Yellow	Yellow	Yellow	Green
Fruit surface	Highly tubercled	Sparsely tubercled	Soft spiny	Soft spiny	Soft spiny	Hard spiny	Pyriform
Nature of epicarp (ripening)	Delicate	Delicate	Delicate	Delicate	Delicate	Shell like - leathery	Papery
Seed shape	Subtridentate	Round oval	Subglobose	Cog wheel	Cog wheel	Cog wheel	Round oval

Table 4.4 Comparative morphology of *Momordica* species of South–East Asia

Characters	*M. clarkeana*	*M. rumphii*	*M. denticulata*	*M. denudata*	*M. subangulata* subsp. *subangulata*
Life span	Perennial	Perennial	Perennial	Perennial	Perennial
Breeding system	Dioecious	Dioecious	Dioecious	Dioecious	Dioecious
Leaf shape	Ovate	Suborbicular	Ovate-oblong	Ovate-lanceolate	Ovate-reniform
Leaf lobing	Unlobed	Trifoliate	Unlobed	Shallow to deeply lobed	Unlobed
Glands on leaf blade margin	Absent	Absent	Present	Absent	Absent
Male flower inflorescence type	Solitary/ pseudoraceme	Solitary	Solitary/ pseudoraceme	Raceme (1–6/node)	Solitary
Petal colour	Pale yellow	Yellow	Creamy white	Yellow	Yellow/orange
Receptacle tube shape	Cupular	Cupular	Saucer shaped	Cupular	Saucer shaped
Fruit shape	Ovoid	Broadly ovoid-ellipsoid/ subglobose	Ellipsoid oblong	Broadly ovoid	Ovoid ellipsoid
Fruit surface	Smooth	Sparsely muricate	Short spiny-sand paper type	Spiny-soft papillate	With irregularly crested ribs
Pericarp	Hard leathery	Leathery	Leathery	Delicate	Delicate
Seed shape	Elliptic/ subcircular	Circular	Subcircular	Ovoid oblong	Ovoid/oblong/ globose
Seed sculpture	Sculptured	Finely corrugated	Finely sculptured	Not sculptured	Slightly sculptured

M. balsamina. The wild variety of bitter gourd (*M. charantia* var. *muricata*), is often misidentified as *M. balsamina* (Maurya et al. 2007) as it has close morphological resemblance to *M. charantia* var. *muricata.* The clear separation of the monoecious from the dioecious species and close similarities within the monoecious species suggest that both the monoecious species (*M. charantia* and *M. balsamina*) have evolved from a common ancestor and has diverged morphologically from the dioecious species.

The presence of umbilical glands in the petiole of *M. cochinchinensis* was reported as a key character in the description given by Chakravarty (1946). However, materials belonging to *M. subangulata* subsp. *renigera* was often misidentified and referred to as *M. cochinchinensis* as evidenced by several publications (Patnaik and Patnaik 1976; Shadeque and Baruah 1984; Handique 1988; Vijay and Jalikop 1980; Mohanty et al. 1994; Ram et al. 2002; Rasul et al. 2004; Sanwal et al. 2011). *M. subangulata* subsp. *renigera* has extra long fruit stalk when compared with other dioecious species. The flowers of *M. dioica* have smaller petals and do not have basal blotches in their petals which are the main distinguishing character from *M. cochinchinensis* and *M. subangulata* subsp. *renigera* (Bharathi et al. 2009). Among the dioecious species, *M. dioica* and *M. sahyadrica* showed close similarities for most of the traits (except for anthesis time, flower size, calyx colour and fruit size) indicating close relationship between them. Although the calyx colour and fruit morphology of *M. sahyadrica* is closer to *M. subangulata* subsp. *renigera*, petal blotch was absent at the base of petals of *M. sahyadrica*. The specimens of *M. sahyadrica* were

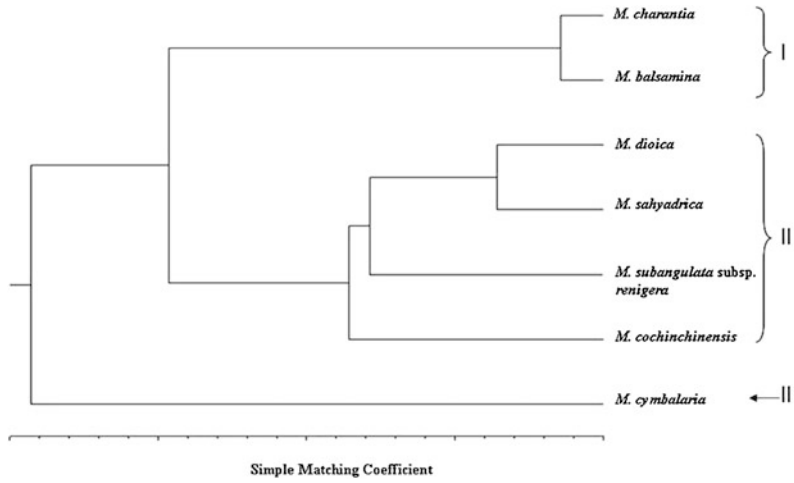

Fig. 4.1 The UPGMA dendrogram based on 40 qualitative characters of *Momordica* species

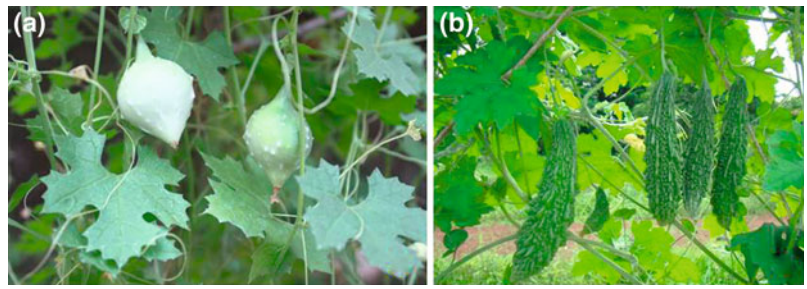

Fig. 4.2 Fruits with muricate-tubercled surface, **a**. *M. balsamina*, **b**. *M. charantia*

placed under *M. dioica* at the Central National Herbarium (CAL), Kolkata due to strong morphological similarity between these two species (Joseph and Antony 2007). However, morphological characters seem to indicate that *M. sahyadrica* is of hybrid origin (Schaefer and Renner 2010).

Analysis of morphological data (50 qualitative and 10 quantitative) for determining the genetic variation within seven *Momordica* species (57 accessions) led to the recognition of three groups (Fig. 4.1; Bharathi 2010). The first group, containing *M. charantia* (var. *charantia*, var. *muricata*) and *M. balsamina* is characterised by $n = 11$, annual, monoecious, non-tuberous roots and muricate—tubercled fruit surface (Fig. 4.2). The second group comprised *M. dioica*, *M. sahyadrica*, *M. subangulata* subsp. *renigera* and *M. cochinchinensis* which is characterised by $n = 14$, perennial, dioecious, tuberous tap roots and echinate—soft papillate fruit surface (Fig. 4.3). The third group contained *M. cymbalaria* which is characterised by $n = 9$, perennial, monoecious, tuberous tap roots and ribbed fruit surface (Fig. 4.4).

Using PCA, the 11 original variables were reduced to three principal components (PC 1–PC 3). PC 1 is represented by fruit weight, fruit length, fruit diameter and 100 seed weight indicating that these variables are related and explain 36.23 % of variation in the data. Leaf length and petiole index were related which together explain 26.04 % variation in the data. In PC 3, petiole length and fruit stalk length together explain 20.59 % variation. A scatter plot on the first two PCs showed that the accessions assigned to the same species are generally grouped together. The obligate cross-pollinated species like *M. cochinchinensis*, *M. subangulata* subsp. *renigera* and *M. sahyadrica* and the facultative cross-pollinated species (*M. cymbalaria*) are well separated. Infra-specific variation was higher in *M. charantia* and formed four distinct groups; the first group comprises

Fig. 4.3 Fruits with echinate—soft papillate fruit surface, **a**. *M. dioica*, **b**. *M. sahyadrica*, **c**. *M. subangulata* subsp. *renigera*, **d**. *M. cochinchinensis*

Fig. 4.4 Fruit of *M. cymbalaria*

the accessions of wild variety (*M. charantia* var. *muricata*); the second contains the accessions of both wild and cultivated varieties. Pusa Do Mausmi (PDM) stands separately in a group, while a wild accession (CHA 1) is clustered with *M. dioica*. The accessions of *M. balsamina* and *M. dioica* also overlap in a group (Bharathi 2010).

Deoxyribonucleic Acid

Advancements in DNA technology have resulted in an array of tools for DNA polymorphism assays. DNA-based molecular markers are useful tools that provide a relatively unbiased estimation of genetic diversity and establish a genetic relation more precisely than morphological and biochemical markers (Soller and Beckmann 1983). Among these, PCR-based random molecular markers such as Random Amplified Polymorphic DNA (RAPDs) and Inter Simple Sequence Repeats (ISSRs) are more commonly used in species in which there is a lack of DNA sequence information. Although a number of varieties belonging to different *Momordica* species have been developed in India, very little information is available about their genetic base.

Understanding the extent of natural variation and phylogenetic relation at molecular level is essential to develop new strategies for genetic improvement of *Momordica*. Although DNA markers are widely used in assessing the phylogenetic relation that they have rarely been used in *Momordica* species. At intra-specific levels relatively few polymorphic markers have been identified in *M. charantia* (Dey et al. 2006; Singh et al. 2007; Gaikwad et al. 2008; Behera et al. 2008) and *M. dioica* (Rasul et al. 2007). The genotypic difference among the varieties of *M. charantia* detected by RAPD was possibly due to their wide geographic distribution, and

considerable ecological and morphological variation with respect to fruit shape, size and colour (Dey et al. 2006). Recently, Wang et al. (2010) developed polymorphic microsatellite markers for *M. charantia* L. to investigate the genetic diversity and population structure within and between *M. charantia* and its four related species (*Cucurbita pepo* L., *Luffa cylindrica* L., *Lagenaria siceraria* L. and *Cucumis sativus* L.).

A combination of 14 RAPD and 7 ISSR informative markers screened by Bharathi et al. (2012a) could precisely identify each of the *Momordica* genotypes and thus it would be of immense value in varietal identification, fingerprinting studies and various genotyping applications in *Momordica*. However, RAPD profiles were found more informative than ISSR profiles in terms of defining varietal identity in *Momordica*. The RAPD and ISSR markers used in this study (Bharathi et al. 2012a) clearly discriminated all the 40 genotypes from each other and resulted in a definitive grouping among different species and varieties of *Momordica* that corresponded well with their known phylogenetic relationships as well as morphological, cytological and taxonomic classifications. The cultivated *M. charantia* and the wild *M. balsamina* being monoecious in nature were clustered closely in one group. The dioecious species of Indian occurrence *M. dioica*, *M. sahyadrica*, *M. subangulata* subsp. *renigera* and *M. cochinchinensis* formed another distinct group. A three-genome phylogeny study (plastid, nuclear and mitochondrial) of *Momordica* (Schaefer and Renner 2010) also grouped the dioecious species of South–East Asia (*M. dioica*, *M. rumphii* [*M. trifolii*], *M. subangulata*, *M. clarkeana*, *M. denudata*, *M. denticulata* and *M. cochinchinensis*) in a single cluster and monoecious species in another single cluster (*M. charantia* and *M. balsamina*). *M. cymbalaria* which has very less similarity with the Asiatic *Momordica* species is grouped with the African species namely *M. kirkii*, *M. boivinii*, *M. humilis* and *M. sessilifolia*.

Higher degree of inter-specific molecular diversity was observed between *M. charantia* and *M. cochinchinensis* (Schaefer and Renner 2010; Bharathi et al. 2012a). The maximum genetic similarity was observed between *M. dioica* and *M. sahyadrica* followed by *M. subangulata* subsp. *renigera* and *M. dioica* and between *M. charantia* and *M. balsamina*. Minimum genetic similarity was observed between *M. charantia* and *M. cochinchinensis*. The relation between *M. dioica* and *M. sahyadrica* was further evident from the interfertile hybrid obtained between these two species (Bharathi et al. 2010a). *M. dioica* was presumed as one of the parents of *M. subangulata* subsp. *renigera* (Bharathi et al. 2010b) and the DNA pattern also indicates the close relation between them. *M. balsamina* showed close similarity to an African species *M. involucrata* (Schaefer and Renner 2010). But among the monoecious annual species, a higher degree of genetic similarity was observed between *M. charantia* and *M. balsamina* (Bharathi et al. 2012a). Occurrence of a high bivalent frequency with normal meiotic cycle in the hybrid progeny of *M. charantia* and *M. balsamina* (Singh 1990) further supported these findings.

Cytology

Karyological studies on the genus are important to enrich the existing knowledge regarding the phylogenetic relations among different species, the evolutionary trends in speciation and taxonomic evaluation. *Momordica* has a basic chromosome number of $x = 9, 11, 14$ and cultivated bitter gourd is diploid ($2n = 22$). All the annual monoecious species had the basic chromosome number of 11; perennial dioecious species had basic chromosome number of 14 while the perennial monoecious species had basic chromosome number of 9. In general, all the species recorded for their common type of chromosomes suggested a common ancestry (Bharathi et al. 2011). *M. charantia* and *M. balsamina* have almost the same number of median and submedian chromosomes although the chromosomes of *M. balsamina* are slightly smaller (Trivedi and Roy 1972). *M. dioica*, a perennial dioecious

species, differs from *M. charantia* and *M. balsamina* in chromosome number as well as through its markedly asymmetrical karyotype (Roy et al. 1966; Trivedi and Roy 1972; Sinha et al. 1997).

Crossability

The cultivated variety of bitter gourd (var. *charantia*) crossed readily with its wild variety (var. *muricata*). The F_1's produced flowers with >80 % stainable pollen and set fruits with abundant seeds from selfed flowers (Agarwal et al. 1957; Joseph 2005; Bharathi 2010). *M. charantia* var. *muricata* does not differ from the true cultivated bitter gourd (*Momordica charantia* var. *charantia*) except for miniature size of fruits and seeds; these were crossed readily and there were many intermediate types (Njoroge and van Luijk 2004). Degner (1947), Walters and Decker-Walters (1988) considered the smaller wild variety (*M. charantia* var. *muricata* syn. with *M. charantia* var. *abbreviata* Ser.) as the progenitor of cultivated bitter gourd.

Hybrid seeds are apparently much more difficult to obtain between *M. charantia* × *M. balsamina* and the reciprocal crosses failed. Nevertheless, F_1 hybrids are highly fertile (54–62 % stainable pollen) and the progeny had a high bivalent frequency with normal meiotic behaviour, suggesting that *M. charantia* have high genetic affinity with *M. balsamina* and thus are intimately related, but they probably stabilised by reproductive isolation due to fertilisation barriers (Singh 1990). These results coupled with morphological (Pandey et al. 2007), karyomorphological (Trivedi and Roy 1972; Bharathi et al. 2011) and molecular (Bharathi et al. 2012a) results reinforce the viewpoint that *M. charantia* and *M. balsamina* are distinct but closely related species (Pandey et al. 2007). However, *M. charantia* was also reported to be closer to the African species *M. angolensis*, and *M. balsamina* was reported closer to *M. welwitschii* (Schaefer and Renner 2010) and *M. foetida* (Ali et al. 2010).

Close affinity between *M. dioica* and *M. sahyadrica* have been reported based on molecular markers (Ali et al. 2010; Bharathi et al. 2012a) as well as morphological markers (Joseph and Antony 2010) and karyomorphological similarity (Bharathi et al. 2011). *M. sahyadrica*, endemic to the Western Ghats of India showed closer morphological similarity to *M. dioica* [considered to be the progenitor of *M. sahyadrica* (Behera et al. 2011; Joseph 2005)] than to other species (Joseph and Antony 2007). High fruit set and fair stainability of inter-specific hybrids between *M. dioica* and *M. sahyadrica* indicated a close relation between these two species. *M. dioica* and *M. sahyadrica* are crossable with *M. cochinchinensis* in one direction, i.e. *M. dioica* and *M. sahyadrica* as female parent (Mondal et al. 2006; Bharathi et al. 2010a, b).

M. dioica and *M. cochinchinensis* are suggested as putative parents of *M. subangulata* subsp. *renigera* (Bharathi et al. 2010b) through morphology and chromosome pairing behaviour of inter-specific hybrids of *M. subangulata* subsp. *renigera*, *M. dioica* and *M. cochinchinensis*. It was further observed that, *M. subangulata* subsp. *renigera* was the only species which had reproductive compatibility in both the directions with *M. cochinchinensis*. It indicated that *M. cochinchinensis* is closer to *M. subangulata* subsp. *renigera* than to any other species. It is considered that *M. subangulata* subsp. *renigera*, the most recent derivative from their diploid ancestors, may not have diverged genetically to that extent so as to create absolute barriers to crossing.

The sect. *Raphanocarpus* is represented in India by only one taxon (*M. cymbalaria*). It had an isolated position and is reported to be closer to the African species like *M. humilis*, *M. kirkii*, *M. boivinii* and *M. sessilifolia* (Schaefer and Renner 2010) and to *M. cabraei* (Ali et al. 2010). *M. cymbalaria* was neither crossable with the sect *Cochinchinensis* nor with sect. *Momordica*. Bharathi et al. (2012a) highlighted its distinctness from other *Momordica* species of Indian occurrence based on molecular and

karyomorphological evidence. It is possible that *M. cymbalaria* that originated along with other African species from a progenitor species differs from the dioecious *Momordica* species of Indian occurrence.

There have been few attempts to raise crosses between sects. Crosses were made between *M. charantia*, *M. balsamina* (sect. *Momordica*) and *M. dioica* (sect. *Cochinchinensis*) exploring possibilities of transferring the desirable attributes of the latter (especially the 'bitterless' trait) to the former but none succeeded (Roy et al. 1966; Joseph 2005) indicating the lack of genetic affinity between them. *M. charantia* and *M. balsamina* failed to cross with dioecious species indicating that they are genetically distantly related and had evolved along a separate line diverging from dioecious species.

Five major patterns of crossing behaviour emerged from the results of the crossing experiments in *Momordica* spp. of Indian occurrence (Bharathi et al. 2012b).

(i) Cross compatible with pollen fertility (*M. charantia* var. *charantia* × *M. charantia* var. *muricata* and *M. dioica* × *M. sahyadrica*).
(ii) Partially compatible with pollen fertility (*M. charantia* × *M. balsamina*).
(iii) Cross compatible with pollen sterility [between diploid species (*M. dioca*, *M. sahyadrica*, *M. cochinchinensis*) and tetraploid species (*M. subangulata* subsp. *renigera*)].
(iv) Partially compatible with pollen sterility (*M. dioica* × *M. cochinchinensis* and *M. sahyadrica* × *M. cochinchinensis*) and
(v) Cross incompatible (between sect.).

Cucurbitacins/Seed Fat

The seed fat of the genus *Momordica* contains alpha-eleostearic acid which is characteristic of this genus. *M. charantia* contains 43.7 % (Khan and Ilyas 1962) to 46.7 % (Hilditch and Williams 1964) and *M. dioica* contains 54.9 % (Hilditch and Williams 1964) alpha-eleostearic acid. From a taxonomic viewpoint, it is noted that all species (three species of each) of *Momordica* and *Trichosanthes* reported have conjugated oils (Chisolm and Hopkins 1964). Seed fat of *M. tuberosa* (=*L. tuberosa)* contains a conjugated triene acid which is characteristic of seed fat of the genus *Momordica*, however, on the other hand, genus *Luffa* does not contain conjugated triene acid (Azeemoddin and Rao 1967) which supported the retention of *L. tuberosa* under the genus *Momordica*.

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