

Floral morphology and systematics of the genus *Thottea* Rottb. (Aristolochiaceae) from the Western Ghats, India

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Abstract The medicinal genus *Thottea* (Aristolochiaceae) is represented in the Western Ghats, India, by eight species, seven of which are endemic to this region. In the present study, diversity in floral structure and organization of these eight species was analyzed from a systematic perspective. Floral morphology was thoroughly studied and discussed with emphasis on 16 qualitative and 11 quantitative characters. Statistical tools such as UPGMA cluster analysis, PCoA, PCA, and one-way ANOVA were used for elucidating species boundaries and inter-relationships. Significance of the selected qualitative and quantitative characters for species level systematics was revealed by the PCA and one-way ANOVA. Based on the nature of sepals (free/fused), two species groups were identified (first group with *T. duchartrei* and *T. idukkiana*, and the second group with the remaining six species). By considering the number and arrangement of stamens, yet another species grouping was proposed (one with *T. abrahamii* and *T. dinghoui*, and the other with the remaining six species). The UPGMA phenogram and the PCoA scatter plot clearly pointed out the existence of two species groups: the first group with *T. abrahamii*, *T. barberi*, *T. dinghoui*, *T. ponmudiana*, *T. siliquosa*, and *T. sivarajanii*, and the second one with *T. duchartrei* and *T. idukkiana*. With regard to the morphometric tools and the taxonomic key, it does not seem possible to distinguish *T. abrahamii* from *T. dinghoui*, and *T. idukkiana* from *T. duchartrei*.

Keywords Aristolochiaceae · Basal angiosperms · Floral morphology · Piperales · Principal component analysis · Principal co-ordinate analysis · Species key · *Thottea* · UPGMA phenogram

Introduction

Thottea, an Indo-Malayan genus, belongs to the birthwort family, Aristolochiaceae. In India, the genus is restricted to the southern region, with ten species. Two of them (*T. tomentosa* and *T. paucifida*) occur on the Andaman Islands (Vasudeva Rao 1986; Mathew 1988; Sumathi et al. 2004), one species (*T. siliquosa*) is distributed throughout the Peninsular India and Sri Lanka (Udayan and Balachandran 2009), and the remaining seven species (*T. abrahamii*, *T. barberi*, *T. dinghoui*, *T. duchartrei*, *T. idukkiana*, *T. ponmudiana*, and *T. sivarajanii*) are strictly endemic to the Western Ghats (Sasidharan 2004; Nayar et al. 2006). Therapeutic effects have been identified for many species of *Thottea*. *Thottea siliquosa*, known as alpam, is reported to have traditional medicinal properties (Chopra et al. 1956; Panse and Nayak 1971; Chelladurai and Apparanantham 1983; Anonymous 1985; Ambasta 1986; Binu 1999; Manilal 2003; Nair et al. 2004; Thirugnanasampandan et al. 2008), and it is one of the components in a medicinal preparation developed for inducing apoptosis (Subbiah 2005).

Thottea species from the Western Ghats are unusual because of their wide range of morphological diversity. Some newly reported species such as *T. abrahamii* and *T. idukkiana* are found to be indistinguishable from the closest relatives and some important diagnostic features are found to vary inconsistently (Renuka and Swarupanandan 1986; Nazarudeen and Sabu 2002; Santhoshkumar et al. 2002). It was difficult to distinguish some species by their

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diagnostic characters mentioned in the species protologues, which indicates the inconsistency of previous species-delimiting characters in *Thottea*. This produces a serious taxonomic chaos. Since most of the species descriptions in *Thottea* are based on floral characteristics, a thorough investigation of the floral features is highly warranted. When none of the tested features can define a taxonomic species boundary, and if one species is seen in close association or overlapping with related species, a re-evaluation is required. Hence, an attempt has been made to study the floral features of *Thottea* spp. from the Western Ghats from a systematic perspective.

Materials and methods

Twenty-one accessions belonging to eight species of *Thottea* were selected for the study (Table 1). The study was confined to the flowering period ranging from December to March in three consecutive flowering seasons. Twenty-five flowering plants were randomly selected at variable distance intervals (always >0.5 m) within each accession. To avoid phenological differences between individuals, plants that had started to bloom were chosen, and the flowers for study were collected at the anthesis stage. The number of flowers studied was at least 100 in all accessions. Floral traits were studied with the help of hand

lens and stereo zoom microscope (SZ61, Olympus, Tokyo, Japan). Photographs were taken with a digital camera (DP11, Olympus, Tokyo, Japan) attached to the microscope. A datasheet was designed, and information was recorded for 16 qualitative and 11 quantitative characters (Table 2). To evaluate significant differences in quantitative traits, one-way ANOVA was performed. A correlation-based PCA was performed to select taxonomically significant qualitative and quantitative characters and to detect outliers. The relative taxonomic distance between the accessions was calculated by cluster analysis. Pairwise relationships were estimated by the Euclidean distance coefficient. The distance matrix was represented as a phenogram by UPGMA clustering method (Sneath and Sokal 1973). PCoA was done for the scaling or ordination of accessions. Two-dimensional scatter plots were constructed based on the PCoA outputs. All statistical tests except ANOVA were performed with the MultiVariate Statistical Package (MVSP) version 3.1 (Kovach Computing Services, Wales, UK). ANOVA was carried out with SPSS 7.5 (SPSS, Chicago, IL, USA).

Results

Flowers of *Thottea* are bracteate, pedicellate, and monochlamydeous (Figs. 1a–b, f–g, l–m, o–p; 2a–b, h–i, l–m,

Table 1 Details of plant materials in the study

Accession no.	Botanical name	Voucher no.	Collected from
1	<i>T. abrahamii</i> Dan et al.	5780	Braemore, Thiruvananthapuram
2	<i>T. abrahamii</i> Dan et al.	5560	Palode, Thiruvananthapuram
3	<i>T. barberi</i> (Gamble) Ding Hou	5594	Chemmunji Hills, Thiruvananthapuram
4	<i>T. barberi</i> (Gamble) Ding Hou	5643	Athirumala, Thiruvananthapuram
5	<i>T. dinghoui</i> Swarup.	5593	Achankovil, Kollam
6	<i>T. dinghoui</i> Swarup.	5561	Palode, Thiruvananthapuram
7	<i>T. duchartrei</i> Sivar., Babu and Indu	5630	Athirapally, Thrissur
8	<i>T. duchartrei</i> Sivar., Babu and Indu	5699	Kottakkal, Malappuram
9	<i>T. idukkiana</i> Pandura. and Nair	5785	Thenmala, Kollam
10	<i>T. idukkiana</i> Pandura. and Nair	5690	Moozhier, Pathanamthitta
11	<i>T. idukkiana</i> Pandura. and Nair	5695	Mullumala, Kollam
12	<i>T. idukkiana</i> Pandura. and Nair	5589	Kariavattom, Thiruvananthapuram
13	<i>T. idukkiana</i> Pandura. and Nair	5697	Nilakkal, Pathanamthitta
14	<i>T. ponmudiana</i> Sivar.	5610	Kallar, Thiruvananthapuram
15	<i>T. ponmudiana</i> Sivar.	5644	Karamanayar, Thiruvananthapuram
16	<i>T. ponmudiana</i> Sivar.	5641	Attayar, Thiruvananthapuram
17	<i>T. siliquosa</i> (Lam.) Ding Hou	5591	Palode, Thiruvananthapuram
18	<i>T. siliquosa</i> (Lam.) Ding Hou	5612	Kallar, Thiruvananthapuram
19	<i>T. siliquosa</i> (Lam.) Ding Hou	5782	Braemore, Thiruvananthapuram
20	<i>T. sivarajanii</i> Santhosh, Shanavas et. Binu	5625	Pothundy, Palghat
21	<i>T. sivarajanii</i> Santhosh, Shanavas et. Binu	5633	Pookkode, Wyanadu

Table 2 List of floral characters analysed

Qualitative traits		
No.	Characters	Character states
1	Flower color	'0' yellow; '1' reddish purple; '2' deep purplish; '3' purplish yellow
2	Eye-shaped dark mark on the adaxial perianth	'0' absent; '1' present
3	Circular protrusions on the perianth	'0' absent; '1' present
4	Nature of perianth	'0' free; '1' fused completely; '2' fused up to the middle
5	Shape of perianth	'0' campanulate (bell-shaped with free sepals); '1' cup-shaped (fused perianth with narrow base and wide mouth); '2' urceolate (fused perianth looking like an urn, with swollen middle and narrowing top); '3' bell-shaped with fused sepals
6	Shape of sepals	'0' orbicular (rounded and flat); '1' orbicular-obovate (shape in between ring and egg); '2' broad orbicular (broad circular); '3' suborbicular (almost circular)
7	Apex of sepals	'0' acute; '1' acuminate; '2' rounded
8	Margin of sepals	'0' not applicable as perianth fused; '1' reflexed; '2' not reflexed
9	Position of anther on the connective	'0' abaxial; '1' adaxial
10	Nature of stamens	'0' free; '1' consistently in three groups; '2' inconsistently in three or more groups
11	Gynostemium	'0' absent; '1' present
12	Contrasting color display in filament and connective	'0' absent; '1' present
13	Appendages on gynostemium	'0' absent; '1' present
14	Bifid stylar lobes	'0' absent; '1' present
15	Flower with more-or-less three sepals	'0' absent; '1' present
16	Ovary wall	'0' glabrous; '1' pubescent
Quantitative traits		
No.	Characters	
1	Perianth diameter	
2	Perianth length	
3	Number of stamens	
4	Number of stylar lobes	
5	Length of anther	
6	Width of anther	
7	Length of pedicel including the inferior ovary	
8	Length of flower	
9	Diameter of the ovary at the widest point	
10	Length of ovary locule	
11	Width of ovary locule at the widest point	

p–q). Perianth is trimerous (Figs. 1b, g, m, p; 2b, i, m, q) and pubescent. Anthers are slightly curved (Fig. 1c, n), tetrasporangiate, extrorse, and dehiscence is by longitudinal slits. Ovary is inferior, elongated, and appears as continuation of the pedicel into the flower proper (Figs. 1a, f, l, o; 2a, h, l, p). Placentation is axile (Figs. 1b, g, m, p; 2b, i, m, q), with numerous anatropous, pendant ovules in a single row in L.S. (Figs. 1a, f, l, o; 2a, h, l, p). The ovary is tetracarpellate, syncarpous, and tetralocular (Fig. 1d). Five species in the present study show a gynostemium (Figs. 1v, 2g).

Sepals are fused in *T. duchartrei* and *T. idukkiana* (Figs. 1o, p; 2a, b) forming a distinct perianth tube, while

they are free in the remaining six species (Figs. 1a, b, f, g, l, m; 2h, i, l, m, p, q). The shape of the perianth tube varies in *T. duchartrei* and *T. idukkiana*. It is bell-shaped (in accession 7) or small cup-shaped (in accession 8) in *T. duchartrei*. But in *T. idukkiana*, the perianth tube is small cup-shaped with the lobes completely fused (in accessions 9 and 10) or large cup-shaped with lobes united half way from the base (in accession 11) or large cup-shaped with the lobes completely fused (in accession 12) or urceolate (in accession 13). The number of sepals is three in all the species studied. Variations in this character were observed, however, in *T. barberi* and *T. sivarajanii*. Along

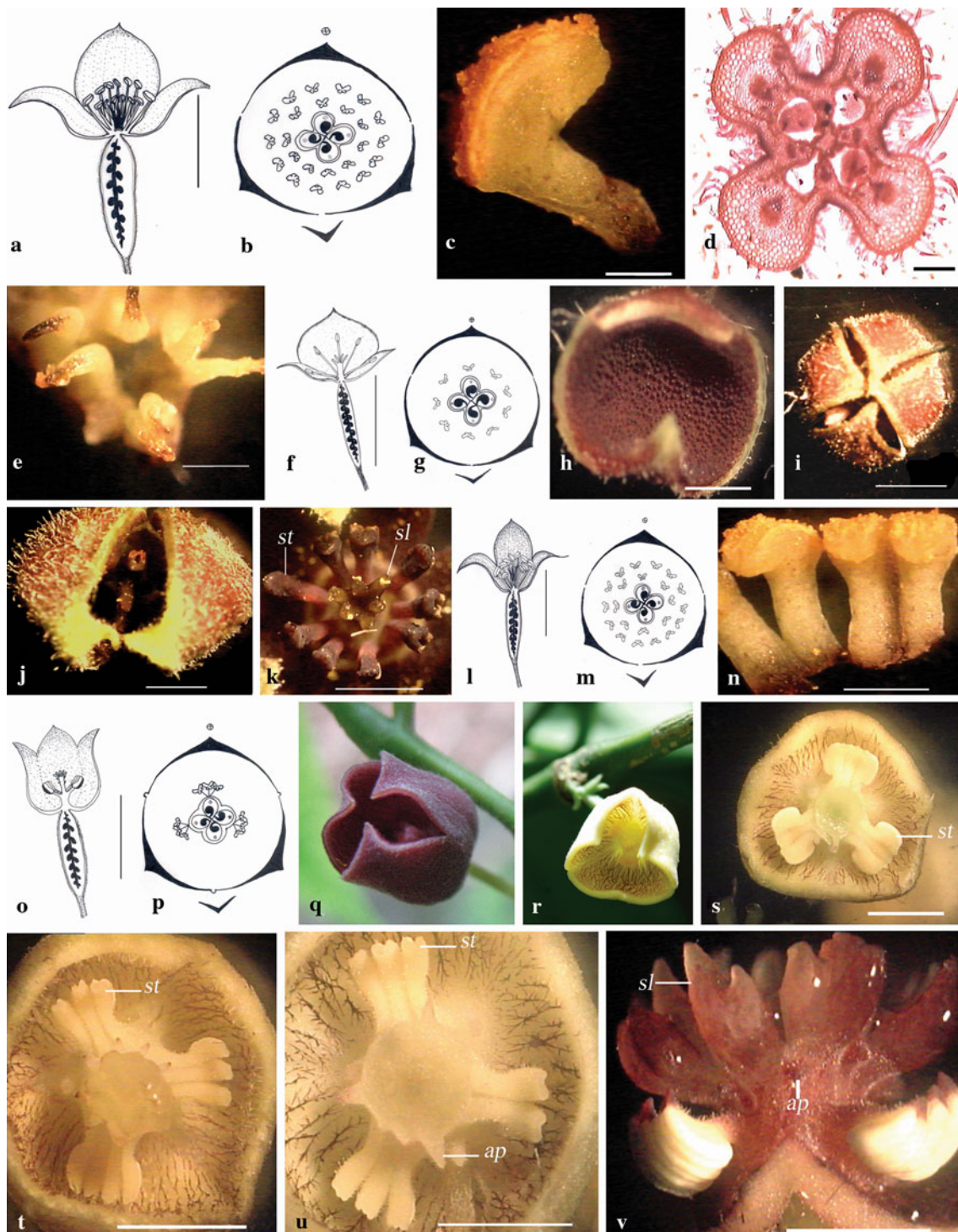


Fig. 1 **a** *T. abrahamii*, flower L.S. (scale 1 cm); **b** *T. abrahamii*, floral diagram; **c** *T. abrahamii*, single stamen (scale 12 mm); **d** *T. abrahamii*, ovary C.S. (scale 200 μ m); **e** *T. abrahamii*, stylar lobes after pollination (scale 10 mm); **f** *T. barberi*, flower L.S. (scale 5 mm); **g** *T. barberi*, floral diagram; **h** *T. barberi*, upper side of the sepal with numerous small circular protrusions (scale 5 mm); **i** *T. barberi*, flower with four sepals (scale 10 mm); **j** *T. barberi*, flower with two sepals (scale 5 mm); **k** *T. barberi*, arrangement of stamens and stylar lobes (scale 5 mm); **l** *T. dinghoui*, flower L.S.

(scale 1 cm); **m** *T. dinghoui*, floral diagram; **n** *T. dinghoui*, stamens (scale 3 mm); **o** *T. duchartrei*, flower L.S. (scale 1 cm); **p** *T. duchartrei*, floral diagram; **q** *T. duchartrei*, purple flower; **r** *T. duchartrei*, yellow flower; **s** *T. duchartrei*, stamens arranged in 3 + 3 + 3 pattern (scale 8 mm); **t** *T. duchartrei*, stamens arranged in 3 + 3 + 4 pattern (scale 8 mm); **u** *T. duchartrei*, stamens arranged in 2 + 3 + 3 pattern (scale 5 mm). **v** *T. duchartrei*, gynostemium lateral view (scale 2 mm) (*st* stamen, *sl* stylar lobe, *ap* appendage)

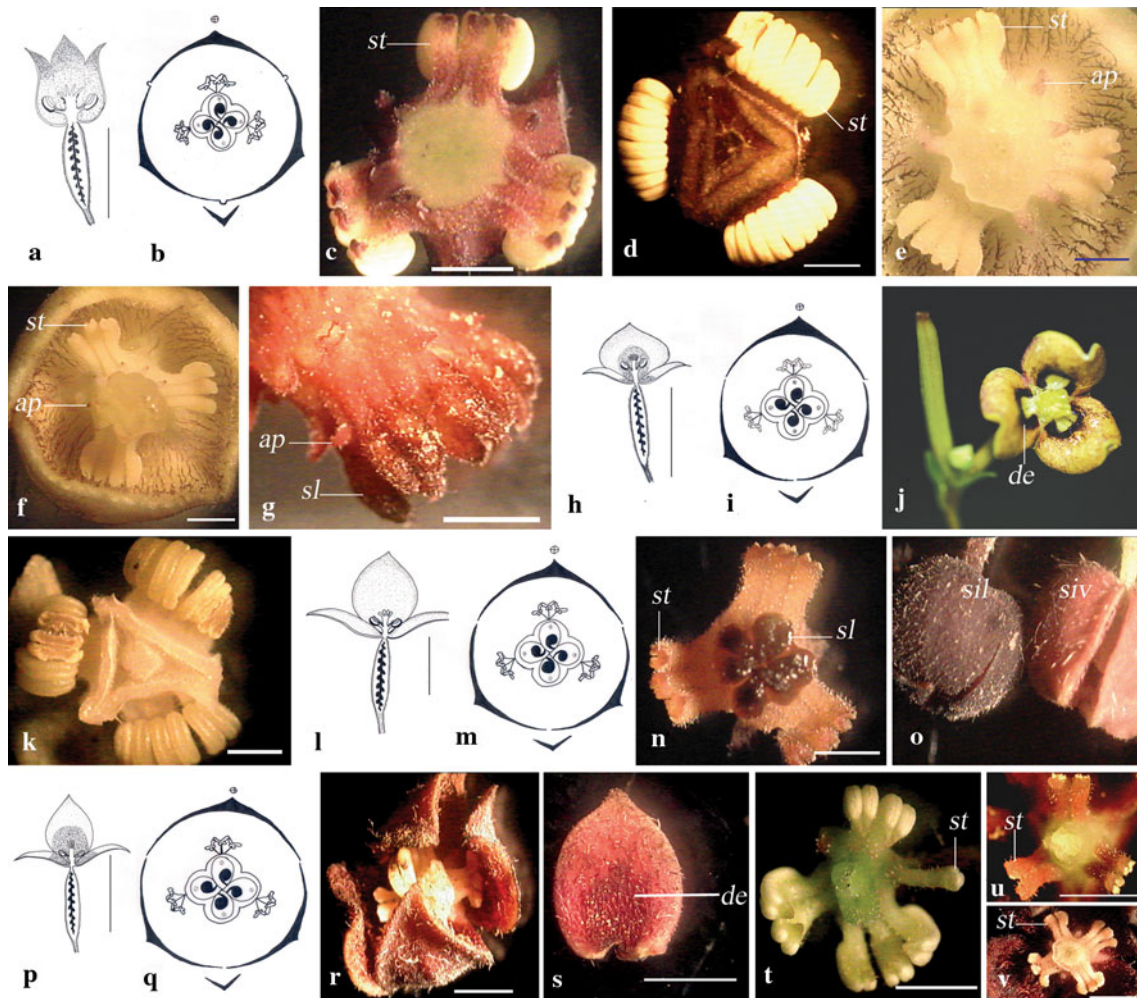


Fig. 2 **a** *T. idukkiana*, flower L.S. (scale 10 mm); **b** *T. idukkiana*, floral diagram; **c** *T. idukkiana*, stamens arranged in 3 + 3 + 3 pattern (scale 4 mm); **d** *T. idukkiana*, stamens arranged in 4 + 4 + 4 pattern (scale 4 mm); **e** *T. idukkiana*, stamens arranged in 3 + 4 + 4 pattern (scale 5 mm); **f** *T. idukkiana*, stamens arranged in 3 + 3 + 4 pattern (scale 5 mm); **g** *T. idukkiana*, gynostemium terminal portion enlarged (scale 5 mm); **h** *T. ponmudiana*, flower L.S. (scale 10 mm); **i** *T. ponmudiana*, floral diagram; **j** *T. ponmudiana*, flower with dark eye on the dorsal surface of the sepal; **k** *T. ponmudiana*, stamens arranged in 3 + 4 + 4 pattern (scale 3 mm); **l** *T. siliquosa*, flower L.S. (scale 5 mm);

m *T. siliquosa*, floral diagram; **n** *T. siliquosa*, stamens (3 + 3 + 3) and styler lobes (scale 2 mm); **o** flowers of *T. siliquosa* and *T. sivarajanii*; **p** *T. sivarajanii*, flower L.S. (scale 5 mm); **q** *T. sivarajanii*, floral diagram; **r** *T. sivarajanii*, flower with four sepals (scale 5 mm); **s** *T. sivarajanii*, sepal with dark eye (scale 3 mm); **t** *T. sivarajanii*, stamens arranged in 3 + 2 + 2 + 1 pattern (scale 1 mm); **u** *T. sivarajanii*, stamens arranged in 2 + 2 + 2 pattern (scale 3 mm); **v** *T. sivarajanii*, stamens arranged in 3 + 3 + 3 + 2 pattern (scale 1 mm) (*st* stamen, *sl* styler lobe, *ap* appendage, *de* dark eye, *sil* flower of *T. siliquosa*, *siv* flower of *T. sivarajanii*)

with the normal trimerous pattern, four (Fig. 1i) and two (Fig. 1j) sepals are seen in some flowers of *T. barberi*. In *T. sivarajanii*, four sepals (Fig. 2r) are seen in some flowers in addition to the flowers with three.

Variations can be noted in the color of the perianth. It is brownish yellow outside and yellowish inside in *T. abrahamii* and *T. dinghoui*. The sepals are reddish purple in *T. barberi* with numerous circular protrusions on the inside (Fig. 1h). In *T. duchartrei*, the sepals are reddish purple in accession 7 (Fig. 1q), but yellowish in accession 9, 10, 11, and 12 of *T. idukkiana*, and broadly orbicular in *T. ponmudiana*. Sepals are acuminate in *T. abrahamii*, *T. barberi*, *T. dinghoui*, and *T. sivarajanii*, while they are acute in *T. duchartrei*, *T. idukkiana*, and *T. siliquosa*.

Sepals are yellow in *T. ponmudiana* with a dark purplish eye-shaped mark in the basal part on the dorsal side (Fig. 2j). Deep purple sepals are seen in *T. siliquosa* (Fig. 2o). The sepals are reddish purple in *T. sivarajanii* (Fig. 2o) with a dark purplish eye-shaped mark in the basal part on the dorsal side (Fig. 2s). The sepals are orbicular-ovate in *T. abrahamii*, *T. dinghoui*, *T. duchartrei*, and accession 13 of *T. idukkiana*; suborbicular in *T. barberi* and *T. sivarajanii*; orbicular in *T. siliquosa* and accessions 9, 10, 11, and 12 of *T. idukkiana*, and broadly orbicular in *T. ponmudiana*. Sepals are acuminate in *T. abrahamii*, *T. barberi*, *T. dinghoui*, and *T. sivarajanii*, while they are acute in *T. duchartrei*, *T. idukkiana*, and *T. siliquosa*.

In *T. ponmudiana*, the sepals are either obtuse or rounded, and the margins of these sepals are reflexed.

A distinct gynostemium is present in five out of the eight species studied (*T. duchartrei*, *T. idukkiana*, *T. ponmudiana*, *T. siliquosa*, and *T. sivarajanii*). The gynostemium is seen as a compound structure formed by the fusion of the upper portion of the syncarpous gynoecium (i.e., without the inferior ovary) and the stamens. At the apex, this structure is divided into a number of stylar lobes (Figs. 1v, 2g). This specific structure is absent in *T. abrahamii*, *T. barberi*, and *T. dinghoui*.

The number and arrangement of stamens differ throughout the species studied. In *T. abrahamii* and *T. dinghoui*, the number varies from 15 to 30. They are free, biserially arranged with 11–17 stamens in the outer whorl and 4–13 in the inner whorl (Fig. 1b, m). The number of stamens varies within the flowers of the same plant, and even within the flowers of the same inflorescence. In *T. barberi*, 9 free stamens are present in flowers with three sepals (Fig. 1g), 6 in flowers with two sepals, and 12 in flowers with four sepals. In the remaining five species (*T. duchartrei*, *T. idukkiana*, *T. ponmudiana*, *T. siliquosa*, and *T. sivarajanii*), mostly nine stamens are arranged as three bundles of three each (3 + 3 + 3 pattern) (Figs. 1p, s; 2b, c, i, m, n, q). More rare or exceptional are the patterns 3 + 3 + 4, 2 + 3 + 3, 4 + 4 + 4, 3 + 4 + 4, 3 + 2 + 2 + 1, 2 + 2 + 2, and 3 + 3 + 3 + 2 (Figs. 1t, u; 2d, e, f, k, t, u, v). Small appendages are found on the gynostemium in *T. duchartrei* and *T. idukkiana* (Figs. 1v, 2g), but not in all accessions examined. Anthers are dorsifixed in *T. abrahamii* and *T. dinghoui* (Fig. 1c, n) and ventrifixed in the other species. In *T. barberi*, the distal portion of the stamen filament is deep purple and the lower portion is light purple, which makes the flower more conspicuous (Fig. 1k).

The ovary surface is densely pubescent in all species, except *T. barberi*, where it is glabrous. The stylar lobes are simple and entire in all species, except *T. duchartrei* and *T. idukkiana*, where along with the simple and entire stylar lobes, bifid lobes (Fig. 1v) are also seen. Variations in quantitative parameters are presented in Table 3.

Morphometric analysis

ANOVA

All the quantitative characters were found to be significant (Table 4).

PCA

Qualitative traits In the PCA of qualitative data, 58.8% of the phenetic variance was accounted for by the first principal axis, followed by 19.3% for the second and 11.4% for

the third principal component (Table 5). All the selected qualitative traits were found principally influential in the PCA. The characters “nature of perianth,” “shape of perianth,” “shape of sepals,” “apex and margin of sepals,” “nature of stamens,” “presence/absence of gynostemium,” “presence/absence of appendages on the gynostemium,” and “presence/absence of bifid stylar lobes” were found influential in the most variable first principal component.

Quantitative traits The first principal component accounted for 96.4% of phenotypic variance and the second component for 1.7% (Table 6). All the quantitative floral traits except “width of ovary locule at the widest point” were found to have significant loadings in PCA.

Cluster analysis

The UPGMA phenogram of the qualitative data provided two principal clusters (Fig. 3). The first one consisted of *T. abrahamii*, *T. barberi*, *T. dinghoui*, *T. ponmudiana*, *T. siliquosa*, and *T. sivarajanii*. In this cluster, accessions of *T. abrahamii* and *T. dinghoui* are found irregularly distributed without definite species boundary. Accessions of *T. siliquosa* are found only within this cluster. *Thottea ponmudiana* and *T. sivarajanii* are closely related within the cluster. In the second cluster, the accessions of *T. duchartrei* and *T. idukkiana* were seen without any significant interspecific differences, and accession 13 is found to be distantly related to the rest in this cluster.

PCoA

The first three principal co-ordinate axes contributed a total variance of 84.3% (first axis 48.7%, second axis 23.3%). In the PCoA scatter plot (Fig. 4), coordination was focused on five regions. A true species coordination was seen for *T. siliquosa*. Out of the remaining four coordinations, three were species groups: the first with *T. duchartrei* and *T. idukkiana*, the second with *T. ponmudiana* and *T. sivarajanii*, and the third with *T. abrahamii*, *T. barberi*, and *T. dinghoui*. The fourth was a single member localization, i.e., accession 13 of *T. idukkiana*.

Discussion

The morphological diversity of angiosperm flowers can be dissected into variations in the number, arrangement, and morphology of the floral organs, such as the perianth, androecium, and gynoecium (Doust 2001). Patterns of such variations are unique in basal angiosperms (Endress 1986, 2001). In the genus *Thottea*, floral variations at inter- and intraspecific levels are unusually high. Species of *Thottea*

Table 3 Variations in floral characters, quantitative

Accession	PD	PL	NS	NSL	LA	WA	LP	LF	OD	LL	WL
1	1.15 ± 0.02bcde	0.77 ± 0.01cdefg	21–30i	6–7d	0.09 ± 0.001a	0.03 ± 0.00c	1.93 ± 0.09de	2.70 ± 0.09defgh	1269 ± 0.05k	195 ± 4d	179 ± 2.1d
2	1.20 ± 0.02cde	0.75 ± 0.01fgh	21–30h	6–7cd	0.09 ± 0.001abcd	0.03 ± 0.00c	1.93 ± 0.02e	2.50 ± 0.03cdefg	1257 ± 2.9k	208 ± 4e	189 ± 3.7e
3	0.54 ± 0.01abcd	0.33 ± 0.01cdefg	6–12bc	5–6b	0.10 ± 0.001e	0.05 ± 0.01b	0.72 ± 0.02ab	1.04 ± 0.02bc	1148 ± 4.5de	272 ± 2kl	291 ± 2.7k
4	0.59 ± 0.01bcde	0.33 ± 0.01bc	6–12b	5–7c	0.09 ± 0.001ef	0.05 ± 0.00b	0.65 ± 0.01abc	0.98 ± 0.01cde	1132 ± 4.2d	250 ± 3i	270 ± 2.1j
5	1.01 ± 0.02cde	0.58 ± 0.01gh	15–28g	5–7a	0.10 ± 0.002abc	0.03 ± 0.00cd	2.09 ± 0.04cd	2.67 ± 0.04hi	1255 ± 1.7k	217 ± 4f	159 ± 1.5b
6	1.00 ± 0.02def	0.57 ± 0.01gh	20–30g	5–7a	0.09 ± 0.001ab	0.03 ± 0.00cd	2.11 ± 0.03cd	2.67 ± 0.04hi	1259 ± 2.8k	202 ± 4e	178 ± 2.1d
7	0.86 ± 0.01ef	1.17 ± 0.01efgh	8–10c	7–9f	0.09 ± 0.001ef	0.07 ± 0.00a	1.03 ± 0.01a	2.21 ± 0.01i	1236 ± 10ij	224 ± 2g	210 ± 2.0f
8	0.66 ± 0.01jk	0.54 ± 0.01bcd	9–10d	8–9f	0.10 ± 0.001fgh	0.05 ± 0.00a	0.48 ± 0.01abc	1.03 ± 0.01c	1192 ± 0.8g	222 ± 2fg	220 ± 1.0g
9	0.94 ± 0.01k	1.20 ± 0.01bcde	10–12e	12–14i	0.11 ± 0.001gh	0.05 ± 0.00a	0.81 ± 0.03abc	2.01 ± 0.03c	1214 ± 7.8h	278 ± 1l	233 ± 0.8i
10	0.76 ± 0.02jk	1.24 ± 0.01ab	11–12f	12–14j	0.11 ± 0.001fg	0.06 ± 0.00a	1.05 ± 0.01de	2.29 ± 0.02defg	1217 ± 7.5hi	248 ± 3i	227 ± 1.1h
11	0.93 ± 0.01ghi	0.96 ± 0.02h	10–12e	12–14i	0.12 ± 0.003ef	0.06 ± 0.00a	0.87 ± 0.03cd	1.84 ± 0.04ghi	1223 ± 3.2hi	264 ± 2j	237 ± 1.7i
12	0.90 ± 0.02ij	0.77 ± 0.01ef	10–11e	11–12g	0.11 ± 0.002fg	0.06 ± 0.00a	0.89 ± 0.01e	1.66 ± 0.02fghi	1218 ± 7.4hi	262 ± 2j	235 ± 1.3i
13	0.96 ± 0.01hi	0.87 ± 0.01h	10–12e	12–13h	0.11 ± 0.001ef	0.06 ± 0.00a	0.85 ± 0.01de	1.72 ± 0.02ghi	1251 ± 6.5jk	267 ± 2jk	233 ± 1.4i
14	1.02 ± 0.02fg	0.65 ± 0.01bcd	9c	7–8e	0.09 ± 0.001bcd	0.03 ± 0.00a	1.03 ± 0.01a	1.68 ± 0.01b	1182 ± 9.4fg	252 ± 1i	176 ± 1.2d
15	1.00 ± 0.02gh	0.67 ± 0.01bcdef	8–10c	7–8f	0.09 ± 0.001cd	0.03 ± 0.00a	1.07 ± 0.01ab	1.74 ± 0.01ab	1166 ± 8.5ef	236 ± 2h	154 ± 0.7b
16	0.85 ± 0.01ghi	0.63 ± 0.01bc	9–10c	7–8e	0.09 ± 0.001d	0.03 ± 0.00a	1.03 ± 0.01abc	1.67 ± 0.01a	1163 ± 11e	207 ± 1e	156 ± 0.9b
17	0.78 ± 0.01a	0.56 ± 0.02defgh	9c	5–7c	0.08 ± 0.001abcd	0.03 ± 0.00cd	0.56 ± 0.02a	1.12 ± 0.03cdef	652 ± 9b	43 ± 0.5a	40 ± 0.3a
18	0.85 ± 0.01ab	0.58 ± 0.01fgh	9c	5–6c	0.08 ± 0.001cd	0.03 ± 0.00d	0.57 ± 0.02a	1.40 ± 0.02cde	645 ± 6ab	41 ± 0.2a	41 ± 0.3a
19	0.85 ± 0.01abc	0.59 ± 0.01bcde	9c	5–6c	0.09 ± 0.001ef	0.03 ± 0.00d	0.56 ± 0.01ab	1.15 ± 0.01fghi	630 ± 5a	43 ± 0.5a	42 ± 0.3a
20	0.71 ± 0.01cde	0.33 ± 0.01a	9a	4–6b	0.09 ± 0.001gh	0.03 ± 0.00c	0.46 ± 0.01bcd	0.79 ± 0.01cdef	883 ± 1.9c	170 ± 1c	170 ± 1.2c
21	0.86 ± 0.02de	0.55 ± 0.01a	6–8a	4–6b	0.09 ± 0.001h	0.032 ± 0.00a	0.49 ± 0.01bcd	1.04 ± 0.02efghi	888 ± 1.4c	154 ± 1b	158 ± 0.9b

PD Perianth diameter, PL perianth length, NS number of stamens, NSL number of stylar lobes, LA length of anther, WA width of anther, LP length of pedicel, LF length of flower, OD ovary diameter, LL length of locule, WL width of locule
 Values followed by the same letters are not significantly different ($p = 0.05$)

Table 4 One-way ANOVA of floral features, quantitative

Variable	<i>N</i>	<i>F</i>	<i>df</i>	<i>p</i>
Diameter of perianth	100	600	20	0.001
Length of perianth	100	2,931	20	0.001
Number of stamens	100	2,051	20	0.001
Number of stylar lobes	100	3,141	20	0.001
Length of anther	100	347	20	0.001
Width of anther	100	1,767	20	0.001
Length of pedicel	100	1,625	20	0.001
Length of flower	100	1,847	20	0.001
Diameter of ovary	100	1,189	20	0.001
Length of locule	100	1,180	20	0.001
Width of locule	100	1,865	20	0.001

N Sample size, *F* F value, *df* degrees of freedom, *p* statistical significance

have a single-whorled perianth with three petaloid organs. A single-whorled perianth is usually called a calyx (Cronquist 1981, 1988), which is applicable to Aristolochiaceae in general (Leins and Erbar 1985; Cronquist 1988; Tucker and Douglas 1996; Takhtajan 1997; González and Stevenson 2000a) and to *Thottea* in particular. González and Stevenson (2000a) gave convincing evidence for an ancestrally single-whorled perianth in Aristolochiaceae, depending on the homology of petals in *Saruma*. Young petals of *Saruma* bear characteristics of stamens in their initiation sequence and shape (Leins and Erbar 1995; González and Stevenson 2000a). The occasional vestigial anthers or “petals” of *Asarum* (Kelly 2001) support an interpretation of these organs as staminodes (Baillon 1860). This again was supported by Ronse De Craene et al. (2003), who stated that the perianth of Piperales is ancestrally single-whorled. In *Thottea*, three distinct perianth primordia are present in a single whorl (Leins et al. 1988). In the present study, species-specific variations were not seen, and thus this can be considered as a general character for the genus.

Thottea shows floral trimery, with some irregularities in *T. barberi*, where some flowers are dimerous or tetramerous. This is in line with the unusual variation in merism in other basal angiosperms (Endress 1986). It would be interesting to know under what conditions the flowers of *Thottea* have a dimerous or tetramerous perianth.

Also the color of the perianth is diverse in *Thottea*. The perianth has a brownish yellow exterior and pure yellow interior in *T. abrahamii* and *T. dinghoui*; reddish purple in *T. barberi* and *T. sivarajanii*; deep purple in *T. siliquosa*; yellowish in *T. ponmudiana*; and both reddish purple and yellowish in *T. duchartrei* and *T. idukkiana*. Thus *T. siliquosa* can be easily identified from the rest because of its color. The variation in perianth color among the accessions of *T. duchartrei* and *T. idukkiana* is interesting.

Table 5 PCA variable loading of floral morphology, qualitative

	Axis 1	Axis 2	Axis 3
Flower color	0.048	0.490 ^a	0.440 ^a
Eye-shaped dark mark on the adaxial perianth	0.062	0.119 ^a	−0.433 ^a
Circular protrusions on the perianth	0.061	0.008	0.189 ^a
Nature of perianth	−0.281 ^a	0.031	0.126 ^a
Shape of perianth	−0.348 ^a	0.128 ^a	0.237 ^a
Shape of sepals	0.520 ^a	0.584 ^a	0.041
Apex of sepals	0.277 ^a	−0.014	−0.435 ^a
Margin of free sepals	0.425 ^a	−0.176 ^a	0.226 ^a
Position of anther on the connective	0.054	−0.310 ^a	0.032
Nature of stamens	−0.339 ^a	0.408 ^a	−0.303 ^a
Gynostemium	−0.116 ^a	0.302 ^a	−0.221 ^a
Contrasting color display in filament and connective	0.061	0.008	0.189 ^a
Appendages in stylar column	−0.244 ^a	0.029	0.103 ^a
Bifid stylar lobes	−0.244 ^a	0.029	0.103 ^a
Flower with more-or-less three sepals	0.061	0.008	0.189 ^a
Ovary wall	−0.061	−0.008	−0.189 ^a
Eigenvalue	3.740	1.226	0.721
Percentage	58.825	19.278	11.345
Cumulative percentage	58.825	78.103	89.448

^a Significantly loaded PCA factors

Table 6 PCA variable loading of floral morphology, quantitative

	Axis 1	Axis 2
Diameter of perianth	0.397 ^a	0.382 ^a
Length of perianth	0.202 ^a	−0.103 ^a
Number of stamens	0.172 ^a	0.396 ^a
Number of stylar lobes	0.202 ^a	−0.333 ^a
Length of anther	0.647 ^a	−0.216 ^a
Width of anther	0.226 ^a	−0.410 ^a
Length of pedicel including the inferior ovary	0.144 ^a	0.440 ^a
Length of flower	0.213 ^a	0.327 ^a
Diameter of ovary at the widest point	0.385 ^a	0.028
Length of locule	0.211 ^a	−0.161 ^a
Width of ovary locule at the widest point	0.049	−0.182 ^a
Eigenvalue	185.346	3.268
Percentage	96.354	1.699
Cumulative percentage	96.354	98.631

^a Significantly loaded PCA factors

With regard to the androecial features, there are two species groups, i.e., species with two stamen whorls (*T. abrahamii* and *T. dinghoui*) and species with a single stamen whorl (*T. barberi*, *T. duchartrei*, *T. idukkiana*, *T. ponmudiana*, *T. siliquosa*, and *T. sivarajanii*). But most species outside the study area (Western Ghats) have two

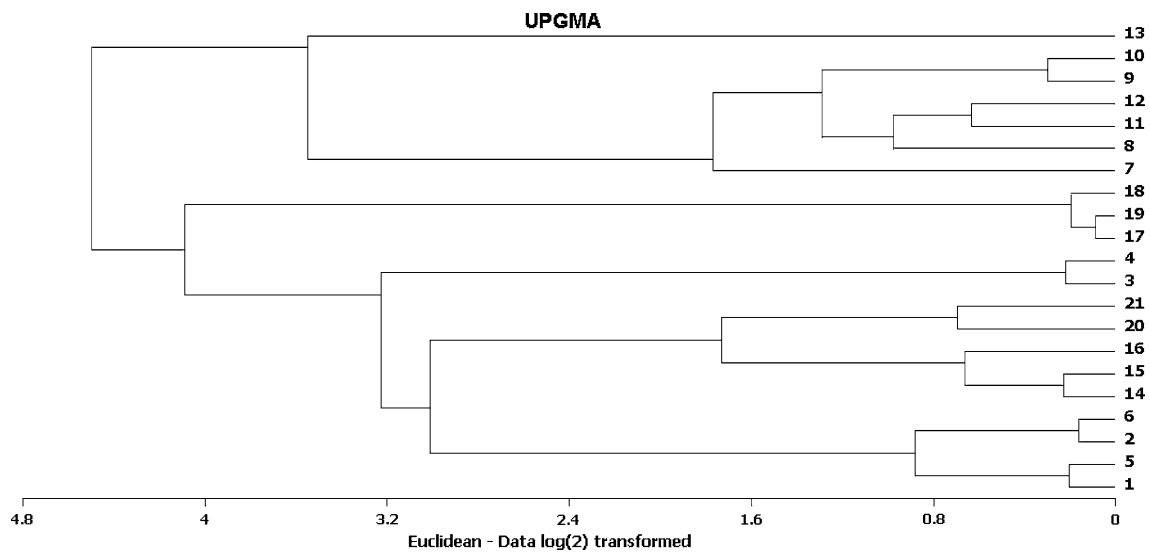


Fig. 3 UPGMA phenogram for 21 accessions of eight species of *Thottea* based on the floral characters. See Table 1 for more information on accessions

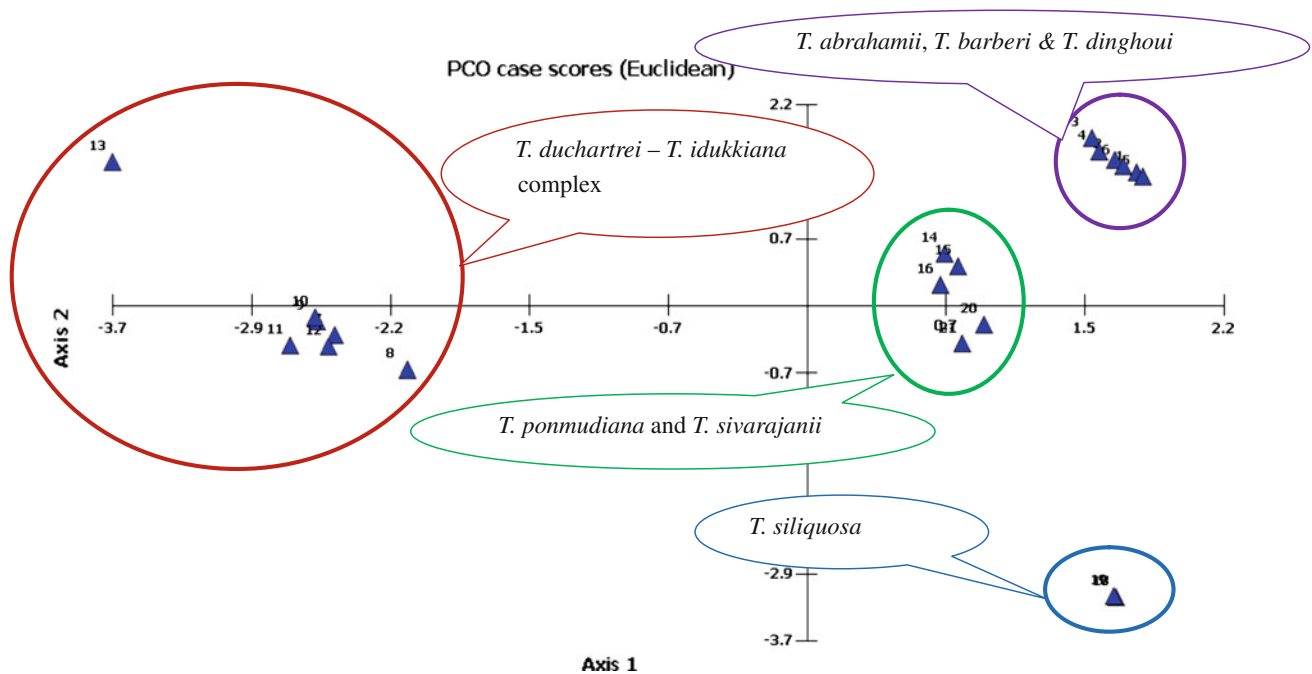


Fig. 4 PCoA scatter plot for 21 accessions of eight species of *Thottea* based on the floral characters. See Table 1 for more information on accessions

stamen whorls (Hou 1981). Based on free or fused stamens, two other groups can be seen, one with free stamens (*T. abrahamii*, *T. barberi*, and *T. dinghoui*), and another with the stamens fused into three bundles. Nine stamens are present in *T. barberi*, *T. duchartrei*, *T. idukkiana*, *T. ponmudiana*, *T. siliquosa*, and *T. sivarajanii*. In contrast, the number ranges from 15 to 30 in *T. abrahamii* and *T. dinghoui*. Based on studies of floral development in *Thottea*, Leins et al. (1988) pointed out that the number of stamens and sterile appendages presumably depends on the

correlation between the size of the organs and the floral apex at the time of initiations. The first available space defines the number and position (frequently alternate) of the organs. When the number is high, all stamens originate more or less simultaneously within one whorl. Multiplication of stamens in one whorl is a sudden evolutionary change. Sugawara (1987), Leins et al. (1988), and González and Stevenson (2000a) regard the horn-like protuberances alternating with the perianth organs in *Thottea* as rudimentary petals. Thus, similar structures

observed here in *T. duchartrei* and *T. idukkiana* may also represent rudimentary petals. According to Leins et al. (1988) the sterile organs of the stylar column may be homologous to either stamens or stigmas in *T. siliquosa*, and to a second stamen whorl in *T. tricornis* and *T. dinghoui*. We were unable to find a homology between these sterile structures and the stigmas in *T. duchartrei* and *T. idukkiana*, and they may represent staminodes. The relatively high plasticity of the androecium in *Thottea* may be a derived character within Aristolochiaceae (Leins et al. 1988). This contradicts the statement of Pandurangan and Nair (1993) in the species protologue of *T. idukkiana*. In basal angiosperms petals or petal-like organs evolved independently in several clades from outer staminodes, such as possibly in *Saruma* (Aristolochiaceae), Winteraceae, and Nymphaeaceae, and the same is true for basal eudicots (Ranunculaceae, Menispermaceae) (Ronse De Craene et al. 2003). Staminodes often arise in angiosperm flowers concomitant with a reduction in stamen number, and they achieve new functions (Ronse De Craene and Smets 2001; Endress and Matthews 2006). The presence of staminodes in *Thottea* may indicate a reduction in the number of functional stamens.

The direction of the thecae is often evolutionarily plastic at lower taxonomic levels (Endress 2001). However, in all species of this study the anthers are extrorse (also in other genera of the family, Endress and Doyle 2009). Another noteworthy aspect is the thick connective and hooded nature of the anthers in *Thottea*. Endress (2001) indicated that a trend to form anthers with thick connectives is prominent in Magnoliales and Laurales. In contrast, in more advanced angiosperms anthers are more elaborate with less sterile tissue, i.e., with thin connectives.

In *Thottea* the gynoecium is syncarpous and the ovary is inferior and elongate. Two carpel whorls are believed to be plesiomorphic for Aristolochiaceae, whereas their closest relatives have only one whorl (Ronse De Craene et al. 2003). *Thottea* also has only one carpel whorl with four carpels. Placentation is axile with a vertical row of anatropous, pendant ovules (see also Igersheim and Endress 1998).

Contrary to the extensive homoplasmy exhibited by the androecium, the gynoecium of Piperales is more uniform in its syncarpy and relatively low carpel number (Tucker et al. 1993; Hufford 1997; Igersheim and Endress 1998). Even the genus *Saururus*, which is sometimes described as apocarpous, is in reality syncarpous (Igersheim and Endress 1998). Eusyncarpy, with carpels fused in the center of the ovary, resulting in axile placentation, evolved independently in Nymphaeaceae, Aristolochiaceae, monocots and, among basal eudicots, in the Trochodendraceae-Buxaceae clade (Endress and Doyle 2009). Maximum likelihood reconstruction of carpel fusion in the basal

angiosperms shows that the syncarpous condition in *Thottea* evolved from partially syncarpous ancestors (Qiu et al. 2000). This syncarpy is considered evolutionarily successful as it enables centralized pollen tube selection (Endress 1982, 1990; Endress et al. 1983).

Presence of a gynostemium (or “stylar column,” Hou 1981), an organ complex that originated by complete fusion of androecium and gynoecium up to the level of the stigma, is an unusual feature in *Thottea* (and other Aristolochioideae). It is especially prominent in *T. duchartrei*, *T. idukkiana*, *T. ponmudiana*, *T. siliquosa*, and *T. sivarajanii*. Since the early 19th century, characters of the perianth and gynostemium have been used extensively in the systematics of Aristolochiaceae (Klotzsch 1859; Duchartre 1864; Huber 1985, 1993). The presence of a gynostemium in magnoliids is unusual because it otherwise occurs in Orchidaceae and Stylidiaceae, two highly derived families. A gynostemium is an extreme manifestation of synorganization (Endress 1990; Specht and Bartlett 2009). According to González and Stevenson (2000b), in *Aristolochia* each gynostemium lobe is formed mostly by extensions of the flanks of two adjacent carpels. This structure has been crucial in the systematics of the subfamily. A preliminary morphological analysis showed that five out of the eight species from the Western Ghats (*T. duchartrei*, *T. idukkiana*, *T. ponmudiana*, *T. siliquosa*, and *T. sivarajanii*) have a well developed gynostemium. The gynostemium ends in a number of stylar lobes. Interestingly, there is no correlation between the number of carpels and stylar lobes, except that there are never fewer stylar lobes than carpels. Some of the stylar lobes are bifid. In *T. duchartrei* and *T. idukkiana*, the stylar lobes are in general erect, but during the receptive stage, they are spreading and wet. In the other species, the lobes are erect, thin, and also wet at the receptive stage. According to Leins et al. (1988), “stylar organs” in the genus *Thottea* do not originally belong to the gynoecium but to the androecium. However, they have a similar stigmatic surface as in *Aristolochia*, and the number that is higher than the carpel number can be explained by forking, which is also indicated by their occasional forking as mentioned above (Igersheim and Endress 1998). In *T. siliquosa* and *T. sivarajanii* the gynostemium is less prominent than in the other three mentioned species with a gynostemium.

Sterile appendages around the gynostemium are characteristic of *T. duchartrei* and *T. idukkiana*. Based on the floral development in four species of *Thottea*, Leins et al. (1988) pointed out that the androecium in *Thottea* is variable, both in number and position of stamens. Even detailed floral developmental studies could not determine whether the sterile organs arising from the gynostemium are homologous to stamens or petals. They may simply be considered as “stylar lobes.” They represent neither staminodes nor the

additional stigmatic row mentioned by Renuka and Swarupanandan (1986) and Pandurangan and Nair (1993).

In the morphometric analyses, PCA showed significant morphological traits for the species/accession level systematics in *Thottea*. In the PCA of qualitative data, characters related to the perianth, androecium, and gynoecium are all present in the most variable first principal axis, which shows their significance in elucidating species relationships in *Thottea*. Perianth morphology has a crucial role inter- and intraspecifically. The same is the case with gynostemium characters. The PCA of quantitative data shows “width of locule at the widest point” as significant. Second most important for species characterization are “length of anther” and “perianth and ovary diameter.”

In the PCoA, four taxonomic groups are identified. The first group is the *T. duchartrei*-*T. idukkiana* complex. The character originally believed to separate the two species, “appendages in the stylar column” (Pandurangan and Nair 1993), did not distinguish the two species based on our material. The second group includes *T. ponmudiana* and *T. sivarajanii*. The eye-shaped marking in the perianth appears to be the principal character that brings these two species together. *Thottea siliquosa* is distinct because of its deep purple flowers and absence of an eye-shaped marking. The fourth group consists of *T. abrahamii*, *T. barberi*, and *T. dinghoui*. In this group, *T. abrahamii* and *T. dinghoui* are indistinguishable in floral structure.

The UPGMA phenogram shows separate clusters for each of the four species, *T. barberi*, *T. ponmudiana*,

characteristics that have not been reported in any other species and that separate this species from the rest. Its isolated position is supported by the morphometric results. *Thottea ponmudiana* and *T. sivarajanii*, although they share the eye-shaped markings on the perianth, appear as different clusters. The phenogram shows two principal clusters: one group with *T. abrahamii*, *T. barberi*, *T. dinghoui*, *T. ponmudiana*, *T. siliquosa*, and *T. sivarajanii*, and a second group with *T. duchartrei* and *T. idukkiana*. This appears to be based on a single character, i.e., free sepals in the first group and sepals fused into a perianth tube in the second group. The PCoA scatter plot also supports this grouping.

Conclusions

The floral morphological features and the morphometric analyses suggest the existence of only six species, in contrast to the eight species described at present. *Thottea barberi*, *T. ponmudiana*, *T. siliquosa*, and *T. sivarajanii* show sound species delimiting characters, while the absence of significant differentiating characters make *T. abrahamii* indistinguishable from *T. dinghoui*, and *T. idukkiana* from *T. duchartrei*. The morphometric analyses clearly point out the existence of two species groups based on the floral morphology.

A taxonomic key is proposed based on floral morphology:

Sepals free-----	
Stamens free-----	
Stamens in single whorl-----	<i>T. barberi</i>
Stamens in two whorls-----	<i>T. abrahamii</i> – <i>T. dinghoui</i> complex
Stamens fused (in three bundles)-----	
Sepals yellow with adaxial eye-----	<i>T. ponmudiana</i>
Sepals reddish purple with adaxial eye-----	<i>T. sivarajanii</i>
Sepals deep purple without adaxial eye-----	<i>T. siliquosa</i>
Sepals fused-----	<i>T. duchartrei</i> - <i>T. idukkiana</i> complex

T. siliquosa, and *T. sivarajanii*. *Thottea abrahamii* is found to be indistinguishable from *T. dinghoui*, and *T. duchartrei* from *T. idukkiana*. *Thottea barberi* is unique owing to the circular projections on the upper side of the tepals and the attractive color display by the stamens,

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References

- Ambasta SP (1986) Useful plants of India. Council of Scientific and Industrial Research, New Delhi
- Anonymous (1985) Wealth of India, raw materials, vol. I. Publications and Information Directorate, Council of Scientific and Industrial Research, New Delhi
- Baillon H (1860) Remarques sur l'androcée des *Asarum* et sur des appendices qui tiennent la place des pétales dans l'*A. europaeum*. *Adansonia* 1:55–57
- Binu S (1999) Ethnobotany of Pathanamthitta District, Kerala, India. Ph.D Thesis, University of Kerala, Thiruvananthapuram
- Chelladurai V, Apparanantham T (1983) Ethnobotany of *Apama siliquosa* Lamk. (*Kuravankanda mooli* Tamil). *Ancient Sci Life* 3:37–39
- Chopra RN, Chopra SL, Nayar SL, Chopra IC (1956) Glossary of Indian medicinal plants. Council of Scientific and Industrial Research, New Delhi
- Cronquist A (1981) An integrated system of classification of flowering plants. Columbia University Press, New York
- Cronquist A (1988) The evolution and classification of flowering plants. New York Botanical Garden, New York
- Doust AN (2001) The developmental basis of floral variation in *Drimys winteri* (Winteraceae). *Int J Plant Sci* 162:697–717
- Duchartre P (1864) Aristolochiaceae. In: De Candolle A-P (ed) *Prodromus systematis naturalis regni vegetabilis*, Paris
- Endress PK (1982) Syncarpy and alternative modes of escaping disadvantages of apocarpy in primitive angiosperms. *Taxon* 31:48–52
- Endress PK (1986) Reproductive structures and phylogenetic significance of extant primitive angiosperms. *Pl Syst Evol* 152:1–28
- Endress PK (1990) Patterns of floral construction in ontogeny and phylogeny. *Biol J Linn Soc* 39:153–175
- Endress PK (2001) The flowers in extant basal angiosperms and inferences on ancestral flowers. *Int J Pl Sci* 162:1111–1140
- Endress PK, Doyle JA (2009) Reconstructing the ancestral angiosperm flower and its initial specializations. *Am J Bot* 96:22–66
- Endress PK, Matthews ML (2006) Elaborate petals and staminodes in eudicots: diversity, function, and evolution. *Org Divers Evol* 6:257–293
- Endress PK, Jenny M, Fallen ME (1983) Convergent elaboration of apocarpous gynoecia in higher advanced dicotyledons (Sapindales, Malvales, Gentianales). *Nord J Bot* 3:293–300
- González F, Stevenson DW (2000a) Perianth development and systematics of *Aristolochia*. *Flora* 195:370–391
- González F, Stevenson DW (2000b) Gynostemium development in *Aristolochia* (Aristolochiaceae). *Bot Jahrb Syst* 122:249–291
- Hou D (1981) *Florae malesiana praecursores LXII*. On the genus *Thottea* (Aristolochiaceae). *Blumea* 27:301–332
- Huber H (1985) Samenmerkmale und Gliederung der Aristolochiaceen. *Bot Jahrb Syst* 107:277–320
- Huber H (1993) Aristolochiaceae. In: Kubitzki K, Rohwer JG, Bittrich V (eds) *The families and genera of vascular plants*. Springer, Berlin
- Hufford L (1997) The roles of ontogenetic evolution in the origins of floral homoplasies. *Int J Pl Sci* 158:S65–S80
- Igersheim A, Endress PK (1998) Gynoecium diversity and systematics of the paleoherbs. *Bot J Linn Soc* 127:289–370
- Kelly LM (2001) Taxonomy of *Asarum* section *Asarum* (Aristolochiaceae). *Syst Bot* 26:17–53
- Klotzsch F (1859) *Die Aristolochiaceae des Berliner Herbariums*. Monatsber Königl Preuss Akad Wiss Berlin 571–625
- Leins P, Erbar C (1985) Ein Beitrag zur Blütenentwicklung der Aristolochiaceen, einer Vermittlergruppe zu den Monokotylen. *Bot Jahrb Syst* 107:343–368
- Leins P, Erbar C (1995) Das frühe Differenzierungsmuster in den Blüten von *Saruma henryi* Oliv. (Aristolochiaceae). *Bot Jahrb Syst* 117(3):365–376
- Leins P, Erbar C, van Heel WA (1988) Note on the floral development of *Thottea* (Aristolochiaceae). *Blumea* 33:357–370
- Manilal KS (2003) *Van Rheede's hortus malabaricus*, English edn., vol 6. University of Kerala, Thiruvananthapuram
- Mathew SP (1988) A supplementary report on the flora and vegetation of Bay Islands, India. *J Econ Tax Bot* 22:249–272
- Nair GM, Rajasekharan S, George V (2004) Final scientific and technical report on pilot participatory programme on conservation and sustainable use of medicinal and aromatic plants. Tropical Botanic Garden and Research Institute, Thiruvananthapuram
- Nayar TS, Beegam RA, Mohanan N, Rajkumar G (2006) Flowering plants of Kerala—a hand book. Tropical Botanic Garden and Research Institute, Thiruvananthapuram
- Nazarudeen A, Sabu T (2002) Staminal instability in *Thottea duchartrei*. *Indian J For* 25:194–195
- Pandurangan AG, Nair VJ (1993) *Thottea idukkiana*—a new species of Aristolochiaceae from Kerala, India. *J Econ Tax Bot* 17:465–467
- Panse MV, Nayak KP (1971) Usefulness of a medicinal plant (*Bragantia wallichii*) in experimental cholera. *Indian J Med Res* 59:1190–1193
- Qiu Y, Lee J, Bernasconi-Quadroni F, Soltis DE, Soltis PS, Zanis M, Zimmer EA, Chen Z, Savolainen V, Chase MW (2000) Phylogeny of basal angiosperms: analyses of five genes from three genomes. *Int J Plant Sci* 161:S3–S27
- Renuka C, Swarupanandan K (1986) Morphology of the flower in *Thottea siliquosa* and the existence of staminodes in Aristolochiaceae. *Blumea* 31:313–318
- Ronse De Craene LP, Smets EF (2001) Staminodes: their morphological and evolutionary significance. *Bot Rev* 67:351–402
- Ronse De Craene LP, Soltis PS, Soltis DE (2003) Evolution of floral structures in basal angiosperms. *Int J Plant Sci* 164:S329–S363
- Santhoshkumar ES, Chitra CR, Shanavaskhan AE (2002) A note on the occurrence of unisexual flowers in *Thottea siliquosa* (Lam.) Ding Hou (Aristolochiaceae). *J Econ Tax Bot* 26:256–258
- Sasidharan N (2004) Biodiversity documentation for Kerala, part 6: flowering plants. KFRI, Peechi
- Sneath PHA, Sokal RR (1973) *Numerical taxonomy*. WH Freeman, San Francisco
- Specht CD, Bartlett ME (2009) Flower evolution: the origin and subsequent diversification of the angiosperm flower. *Annu Rev Ecol Syst* 40:217–243
- Subbiah V (2005) Natural product based apoptosis inducers. Phyto Myco Research Corporation, Greenville, NC, US. <http://www.freepatentsonline.com/20050084547.html>
- Sugawara T (1987) Taxonomic studies of *Asarum sensu lato* III. Comparative floral anatomy. *Bot Mag (Tokyo)* 100:335–348
- Sumathi R, Maina V, Lakra GS (2004) *Thottea paucifida* Ding Hou, family Aristolochiaceae, a new record for India. *J Bombay Nat Hist Soc* 101:195–196
- Takhtajan A (1997) *Diversity and classification of flowering plants*. Columbia University Press, New York
- Thirugnanasampandan R, Mahendran G, Narmatha Bai V (2008) Antioxidant properties of some medicinal Aristolochiaceae species. *Afr J Biotechnol* 7:357–361
- Tucker SC, Douglas AW (1996) Floral structure, development, and relationships of paleoherbs. In: Taylor DW, Hickey LJ (eds) *Flowering plant origin, evolution and phylogeny*. Chapman and Hall, New York

- Tucker SC, Douglas AW, Liang H-X (1993) Utility of ontogenetic and conventional characters in determining phylogenetic relationships of Saururaceae and Piperaceae (Piperales). *Syst Bot* 18:614–641
- Udayan PS, Balachandran I (2009) Medicinal plants of Arya Vaidya Sala Herb Garden. Arya Vaidya Sala, Kottakkal, Malappuram
- Vasudeva Rao MK (1986) A preliminary report on the angiosperms of Andaman and Nicobar Islands. *J Econ Tax Bot* 8:107–184