



Usefulness of morphological characters for infrageneric classification of *Elatostema* (*Urticaceae*)

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Key words

Elatostema
morphology
phylogeny
Procris
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Abstract In 1896, Hans Hallier was the first author to reduce the two genera *Pellionia* and *Procris* to subgeneric status within the genus *Elatostema* (*Urticaceae*). In 1935 and 1936, Hilde Schröter and Hubert Winkler proposed the following four subgenera: subg. *Elatostema*, subg. *Elatostematoides*, subg. *Pellionia* and subg. *Weddellia*, while maintaining *Procris* as a distinct genus. More recently, Wang (1980a) rejected Schröter and Winkler's subgeneric classification of *Elatostema* and proposed a sectional and serial infrageneric classification of recognising as sections *Androsyche*, *Elatostema*, *Laevisperma*, *Pellionioides* and *Weddellia* (as '*Weddellia*'). He maintained both *Pellionia* and *Procris* as distinct genera. All previous researchers of *Elatostema* and related taxa primarily based their classifications on the morphology of leaves, stipules, inflorescence and receptacle. Our analysis, based on similar morphological characters, does not support the previous infrageneric classifications. *Procris* forms a monophyletic clade, nested within a clade consisting of several species of *Elatostema* subg. *Pellionia* and one of subg. *Elatostematoides*. *Elatostema auriculatifolium* (subgeneric classification unclear) is also included within this clade. This clade is sister to the *E. latifolium*–*E. tsoongii* pair of species (also subg. *Pellionia*), subg. *Elatostema* (the remaining species of this subgenus), species of subg. *Weddellia* and *E. rostratum* (subg. *Elatostematoides*). *Elatostema* subg. *Weddellia* is paraphyletic within subg. *Elatostema*. The recognition of *Elatostematoides*, *Pellionia* and *Procris* as distinct genera is not supported.

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INTRODUCTION

Elatostema J.R.Forst. & G.Forst. (*Urticaceae*) is a taxonomically problematic genus of c. 300 species that is widespread throughout the tropical, subtropical and subtemperate regions of Africa through SE Asia, Australasia to Polynesia. The identification and infrageneric classification of *Elatostema* has traditionally been based on morphological characteristics (for example, Robinson 1910, Winkler 1922, Schröter & Winkler 1935, Wang 1980a, b, Weddell 1854, 1856, 1857, 1869). The characters used in this phylogenetic analysis have, in part, been based on the morphological features used by these researchers. However, several features have been re-interpreted so that they can be scored more consistently than is possible for many of the more subjectively defined character states used by previous researchers (for example, venation patterns). A few additional characters, not used by previous workers, have also been included (for example, the form of nanophylls). Multimeric overlapping characters (that is, characters defined by dimensions rather than non-overlapping codes) have been included by conversion to non-overlapping or minimal overlapping characters states using the divergence coding technique of Almeida & Bisby (1984). The following multi-metric characters that were converted include: plant height, petiole length, lamina length, lamina width, lamina length to width ratio, lamina asymmetry, leaf vein pairs and male tepal length. However, stipule length was not used because species with non-persistent stipules usually lose their stipules while they are young and these are frequently smaller than, and hence, not comparable with the older, persistent stipules of other species. Up to five herbarium specimens of each species included in this study were analysed to cover the morphological variation within each species.

Morphological characters used by Robinson (1910)

In species of *Elatostema* (s.s.), the involucre bracts are present and enclose the staminate and pistillate flowers, whereas involucre bracts are absent in *Pellionia* and *Procris*. The pistillate flowers of *Pellionia* are arranged in condensed inflorescences, whereas those of *Procris* are arranged on a fleshy receptacle. The inflorescence of staminate flowers of *Pellionia* and *Procris* are always openly paniculate (Qi et al. 2003, Ariyanti 2004, respectively). Robinson (1910) emphasised the usefulness of the inflorescence and pistillate flowers for differentiating species of *Elatostema*, *Elatostematoides*, *Procris* and *Pellionia*. Robinson (1911) concluded that merosity of the perianth of pistillate flowers was taxonomically useful for distinguishing *Elatostema*, *Elatostematoides*, *Pellionia* and *Procris*, with *Elatostema* characterised by 3-partite pistillate flowers, although 2- and 4-partite perianth flowers also appear to be present in otherwise 3-partite flowered inflorescences. *Elatostematoides* was characterised as having a 5-partite pistillate perianth. However, Robinson mistook the staminodes for the perianth. The perianth is much reduced or absent in all species of *Elatostema* s.str. (Schröter & Winkler 1935). The pistillate perianth of *Pellionia* is 4- or 5-partite and as long as the ovary. The pistillate perianth of *Procris* is 3- or 4-partite, deeply divided, widely spreading, and shorter than or as long as the ovary. Thus, *Pellionia* is indistinguishable from some species of *Procris* and *Elatostematoides*.

The presence or absence of staminodes in pistillate flowers is thus not useful for distinguishing the genera discussed by Robinson. However, this character is taxonomically useful, at a tribal level, for distinguishing the *Elatostemeae* from all other tribes in the family. The pistillate flowers of all genera of *Elatostemeae* have staminodes, whereas the pistillate flowers of all other tribes lack staminodes (Friis 1993). We included perianth merosity in our dataset to test its usefulness in defining taxon relationships.

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Morphological characters used by Schröter & Winkler (1935)

Schröter & Winkler (1935) provided a comprehensive discussion of morphological characters that they regarded as taxonomically useful for understanding *Elatostema* and for distinguishing the four subgenera recognised by them, namely subg. *Elatostema*, subg. *Elatostematoides*, subg. *Pellionia* and subg. *Weddellia*. The morphological characters used by them included features of habit, anisophylly, phyllotaxy, leaf and venation characteristics, cystoliths, stipules and reproductive features (including inflorescence structure, floral and fruiting characteristics). Although promoting the usefulness of these characters, they recognised that the taxonomic circumscription of these four subgenera was often unclear.

The characters and character states discussed by Schröter & Winkler (1935) include:

Vegetative features

Herbs, subshrubs and shrubs — Members of *Elatostema* are mostly herbs or subshrubs, rarely shrubs. The majority of taxa of subg. *Weddellia* and subg. *Elatostema* are fleshy herbs, whereas many of the species of subg. *Pellionia* and subg. *Elatostematoides* have more sclerenchymatous cells in the stem during later growth stages. Therefore, some of these species appear slightly 'woody', here referred to as subshrubs. According to Schröter & Winkler (1935) there are many subshrubs or shrubs in subg. *Pellionia*, but they did not provide specific examples. Species of subg. *Elatostematoides* are all subshrubs.

Leaf characteristics

Anisophylly — The leaf-pairs at each node are characteristically very unequal in size in *Elatostema* such that the foliage appears strongly anisophyllous. This anisophylly is also present in other Urticaceae genera, including *Pilea*. Schröter & Winkler (1935) considered the presence or absence of the nanophyll (small leaves) and its shape as useful taxonomic characters in distinguishing subgeneric groupings within *Elatostema*. In subg. *Weddellia*, all species have shortly petiolate nanophylls, whereas many species in the remaining subgenera lack nanophylls. In subg. *Elatostema*, only three species have nanophylls (namely, *E. ambiguum*, *E. bulbiferum* and *E. burmanicum*). Sessile, minute, more or less linear and readily caducous nanophylls are found in a few species of subg. *Elatostematoides* (for example, a few species of the *Elatostema rostratum* group). Finally, in subg. *Pellionia*, some species have relatively large, green leaf-like nanophylls (for example, *E. filicinum*, *E. raapii* and *E. sinuatum*, and), some others have minute nanophylls (for example, *E. hallieri* and *E. variolaminosum*).

The form of the nanophylls is relatively consistent throughout the genus but has not been used as a taxonomic character by previous researchers. When nanophylls are absent, the normal larger leaves (macrophylls) are spirally arranged. The macrophylls vary in shape from obovate, elliptic, narrowly ovate to ovate or rarely roundish. All normal larger leaves that occur in *Elatostema* and other Urticaceae taxa are here referred to as macrophylls to distinguish them from the much smaller nanophylls inserted at the same nodes. Goebel (1928) observed 'rudimentary leaves' (nanophylls) on newly germinated plants of *E. sessile* (type species of genus), that became fused with the stipule during later stages of growth.

Phyllotaxy — Schröter & Winkler (1935) described the phyllotaxy of *Elatostema* as opposite, decussate, similar to other members of the family. However, since one leaf of the leaf-pair at each node is much reduced compared to the other

leaf, this gives the appearance of an alternate/spiral arrangement.

Leaf shape symmetry — The width of the lamina of the macrophyll on each side of the central axis (from midvein to margin) is unequal.

Leaf base symmetry — The base of the broader side of the macrophyll's lamina usually exceeds the length of the narrower side. Occasionally the base is slightly cordate (for example, *E. hastatum* and *E. reticulatum*) to more fully cordate (rounded on both sides) (for example, *E. griffithianum*).

Leaf venation — Robinson (1910) concluded that it was not possible to categorize the venation patterns found in *Elatostema* because they were too variable. In contrast, Schröter & Winkler (1935) considered venation patterns taxonomically

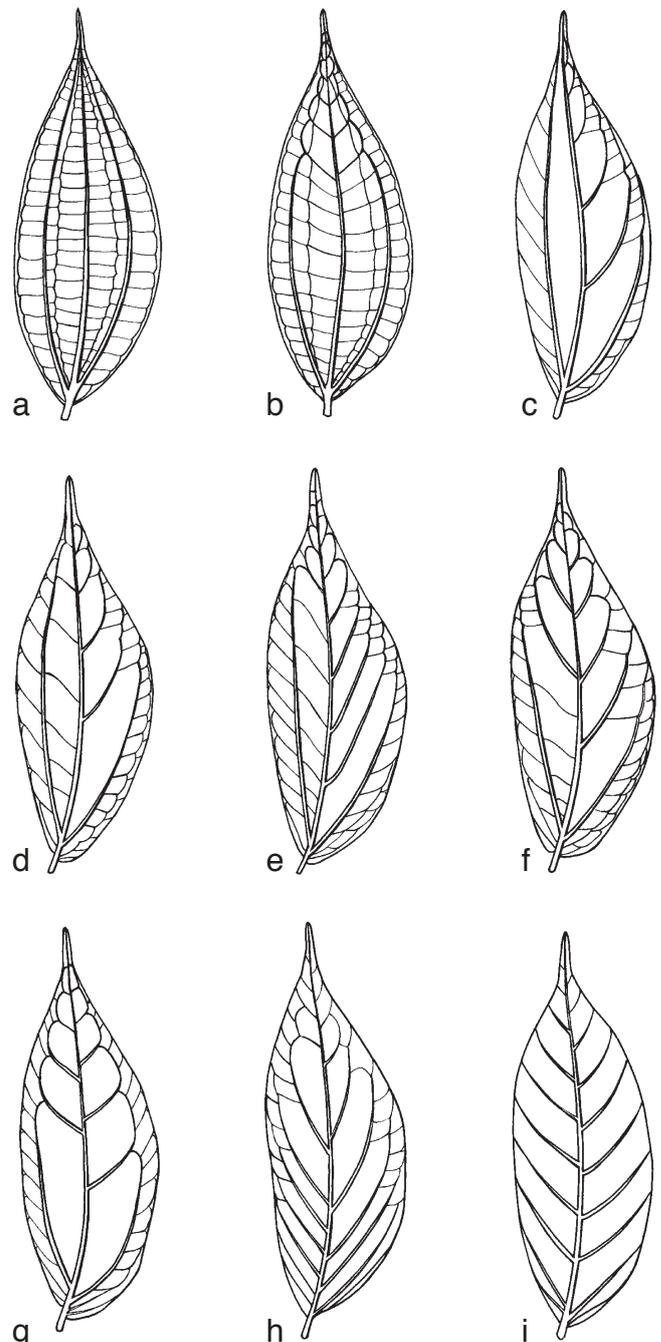


Fig. 1 Venation types redrawn from Schröter & Winkler (1935: f. 3–11). a. Type I, *triplinervis*; b. Type II, *triplinervis supernis penninervis*; c. Type III, *semi-penninervis*; d. Type IVa, *semi-penninervis apex penninervis*; e. Type IVb, *semi-penninervis supernis penninervis*; f. Type IVd, *semi-penninervis supra medium penninervis*; g. Type IVe, *subpenninervis*; h. Type IVe, *subpenninervis*; i. Type V, *penninervis*.

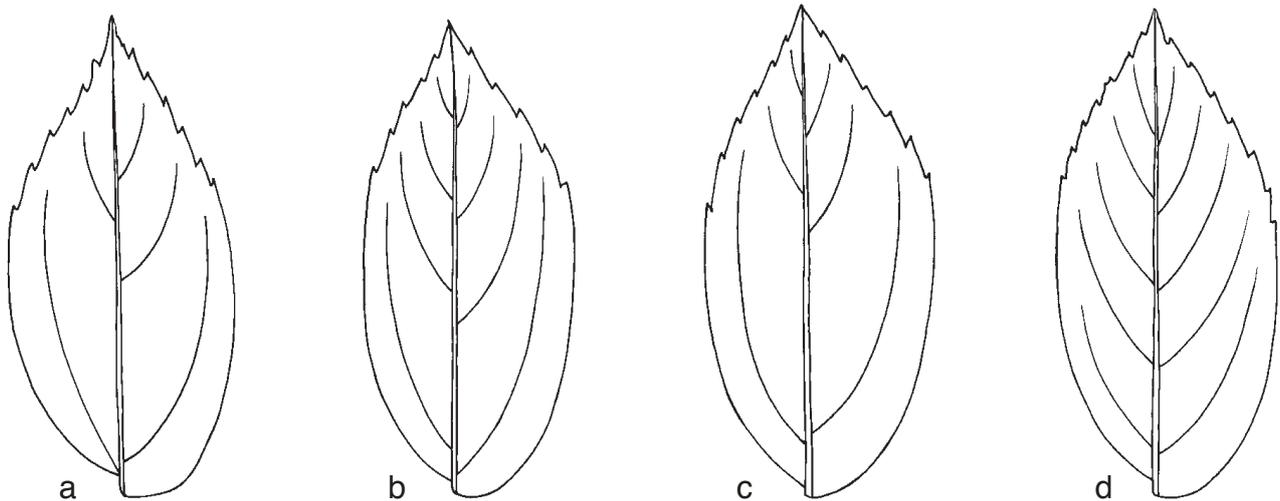


Fig. 2 Classification of venation types as used by Wang (1980); figures redrawn from Wang (1980: 3). a. 3-nerved; b. semi-3-plinerved; c. 3-plinerved; d. penninerved.

useful, and the variability relatively small. They recognised the following five venation types (Fig. 1):

- Type I 3-plinerved (major secondary veins are inserted near base of lamina and converge near apex).
- Type II 3-plinerved with distal part of lamina pinnately nerved (as type I, but major secondary veins in distal third replaced by pinnate venation). *Pilea* is characterised by type I and II. Neither type is found in *Elatostema*.
- Type III semi-pinnately nerved with the two basal lateral secondary veins unequal in length and direction. Only one vein extends to the apex, the other vein is much shorter, directed more towards the margin, and has more lateral secondary veins on this same side. This type III venation (another modification of type I) is found in subg. *Elatostematoides* and in some species of *Pellionia*.
- Type IV semi-pinnately to subpinnately nerved, with five subtypes which appear to be minor variants.
- Type V pinnately nerved on both sides of the central. This type is found in a few species of *Pilea*, in many species of *Pellionia* and all *Procris* species, plus a few species of *Elatostema* s.str. (for example, *E. macrophyllum* and *E. rugosum*).

In his work on the systematics of Chinese species of *Elatostema*, Wang (1980a) simplified the Schröter & Winkler (1935) classification of venation patterns (reproduced here as Fig. 2). He recognised four character states, namely 3-nerved, semi-3-plinerved, 3-plinerved and penninerved.

Cystoliths — Cystoliths are present in all species of the *Urticaceae* (Bigalke 1933) and their form and distribution have been found to be taxonomically useful for distinguishing infra-familial groups, even if only as secondary characters. Within the large genus *Elatostema*, they are, at least, superficially relatively homogeneous. A detailed study of the taxonomic usefulness of cystoliths within *Elatostema* has not been included in this study; however, additional research is recommended.

Stipules — In *Elatostema*, the stipules are usually membranous, occasionally somewhat fleshy, and usually glabrous. They mostly vary from narrowly ovate (lanceolate) to almost linear (often referred to as linear-lanceolate), initially often shorter than mature stipules. Some large-leaved species (for example, *E. fagifolium*, *E. nemorosum* and *E. smilacinum*)

have large stipules of 30–50 mm long. *Elatostema sinuatum* and related species possess short to minute stipules of 1–2 mm long (on macrophylls).

Reproductive features

Inflorescence

The basic inflorescence structure of *Urticaceae* is cymose, either dichasial or monochasial (Golenkin 1894, Bernbeck 1932). Schröter & Winkler (1935) placed considerable taxonomic importance on the various types of inflorescence exhibited by the members of the tribe *Elatostemeae*.

Structure of inflorescence — The inflorescences vary from relatively loosely arranged clusters of flowers (for example, as found in subg. *Elatostematoides* and subg. *Pellionia*) to more crowded inflorescences (for example, *E. velutinum* and *E. undulatum*, both subg. *Pellionia*). The inflorescence of the former group lacks an involucre, whereas the latter group has a slightly developed involucre of bracts. Schröter & Winkler (1935) regarded the arrangement of flowers as a very important character for delimiting subgenera of *Elatostema*.

The male and female inflorescences are 'divided' into a series of compartments with the underlying cymose arrangement maintained (Weddell 1856, Schröter & Winkler 1935: f. 17, 29, 30). Although the latter regarded the female inflorescence of *Elatostema vittatum* (subg. *Elatostematoides*) as compartmentalised ('ordered') (their f. 17), we scored it as 'unordered' because the indistinct compartmentalisation meant that the scoring of this character was problematic.

Schröter & Winkler (1935: f. 18–28) discussed and illustrated the extent of fusion between involucral bracts. We did not use this character because it proved difficult to measure consistently.

Receptacle of inflorescence — The inflorescences of *Elatostema* subg. *Elatostematoides*, subg. *Pellionia* and the genus *Pilea* lack a receptacle (Schröter & Winkler 1935), whereas the receptacle is present for members of subg. *Elatostema*, subg. *Weddellia* and the female inflorescences of *Procris* (absent in male inflorescences of the latter genus).

As for several other morphological characters that Schröter & Winkler (1935) regarded as taxonomically useful, none of their inflorescence features uniquely describe any of the taxa listed in Table 1. There is considerable overlap between the character-states of most characters used to distinguish these taxa.

Table 1 Summary of taxonomically useful inflorescence characters based on usage by Schröter & Winkler (1935: 17 p.p.).

Characters	<i>Pilea</i>	<i>Elatostematoides</i>	<i>Pellionia</i>	<i>Elatostema</i>	<i>Weddellia</i>	<i>Procris</i>
Male inflorescence						
Form	± loose	slightly crowded or loose	± slightly crowded or ± loose	crowded	crowded	loose
Shape	openly branched	slightly head-like or openly branched	slightly head-like or openly branched	head-like (when slightly fused), or disc-shaped (when mostly fused), or concave (as in <i>E. ficoides</i>)	± disc-shaped	openly branched
Receptacle	absent	absent	absent (except slightly developed in <i>E. velutinum</i> and <i>E. undulatum</i>)	present	present	absent
Female inflorescence						
Form	± loose	crowded	± slightly crowded or ± loose	crowded	crowded	crowded
Shape	openly branched	slightly head-like	slightly head-like or openly branched	head-like (when slightly fused), or disc-shaped (when mostly fused), or concave (as in <i>E. ficoides</i>)	± disc-shaped	globular
Receptacle	absent	absent	absent (except to a lower extent in <i>E. velutinum</i> and <i>E. undulatum</i>)	present, distinct (except <i>E. ambiguum</i> , <i>E. bulbiferum</i> , <i>E. umbellatum</i> have no receptacles)	present	present

MATERIAL AND METHODS

Taxon sampling

The taxa of *Elatostema* used in this study represented each of the four subgenera of the genus recognised by Robinson (1910) and Schröter & Winkler (1935), namely, subgenera *Elatostema*, *Elatostematoides*, *Pellionia* and *Weddellia*. Species of *Pilea* and *Procris* (both *Elatostemeae*) were included, along with representatives of the *Boehmerieae*, *Parietarieae* and *Urticeae*. *Boehmeria calophleba* and *B. macrophylla* were used to root the trees.

Management of morphological data

Measurement of morphological characters were recorded and managed in *DeltaAccess* software, v1.9 (Hagedorn 2005), with data exported in DELTA-format. These DELTA files were then converted into NEXUS formatted files using the NDE software (Page 2001). These data were then loaded directly into PAUP* v4.0b10 (Swofford 2002) for phylogenetic analyses.

Choice and definition of characters

We use morphological characters to evaluate the morphological support for the monophyly of the infrageneric groupings in *Elatostema* proposed by Schröter & Winkler (1935, 1936). The choice of characters was based, in part, on the results of Robinson (1910) and Schröter & Winkler (1935, 1936), and, to a lesser extent, on research on other members of the *Urticaceae*. A list of the morphological characters used in this study is given in Table 2. All characters were treated as ordered and polarised to minimise parallel gain (Kitching in Forey et al. 1992).

Non-overlapping characters converted from overlapping characters

Even though overlapping morphometric characters may be useful in defining taxa, the PAUP* v4.0b10 software (Swofford 2002), excludes overlapping characters. There is an implicit assumption in phylogenetic analysis that character states must be discrete (Pimentel & Riggins 1987, Scotland in Forey et al. 1992) but the recognition of distinct character states in overlapping data is frequently difficult. Characters derived from overlapping morphometric data can be used in cladistic analysis (Ariyanti & Conn 2005). However, the transforming of such data into discrete, non-overlapping states has been controversial. One concern with coding overlapping data into discrete, non-overlapping states is that this may result in an unacceptable level of data distortion (Chappill 1989). However, Thiele &

Ladiges (1988), Thiele (1993) and Ariyanti & Conn (2005) maintain that morphometric data can provide useful information in phylogenetic analyses.

Divergence coding (Almeida & Bisby 1984) uses box plots (or 'box-and-whisker' plot sensu Tukey 1977) to represent the median, 1st quartile and 3rd quartile values to separate overlapping data into non-overlapping character states. A box plot provides a simple graphical summary of a set of data. It shows a measure of central location (the median), two measures of dispersion (the range and inter-quartile range), the skewness (from the orientation of the median relative to the quartiles) and potential outliers (marked individually). The lines extending from the box ('whiskers') indicate the range of values within 1.5× inter-quartile range (Wilkinson et al. 1992). We converted quantitative character states to discrete values to eliminate or, at least, minimise the degree of overlap between the character states in the following way: each character was divided into non-overlapping states by placing the inter-quartile range into a single discrete state. Occasionally, characters of some taxa could not be assigned to a single discrete character state. These were recorded as having more than one character state. Five collections of each taxon were used to generate the distributions for the box plots based on minimum and maximum values of each overlapping character. The following characters were recoded using the divergence coding technique: plant height; petiole length; lamina length; lamina width; lamina length to width ratio; veins number; length of tepals in male flowers. The codified values for each of these characters are listed in Table 2.

Phylogenetic analyses

Ten uninformative characters were deleted prior to analysis. Heuristic searches were conducted in PAUP* using tree bisection reconnection branch-swapping restricted to 100 trees per replicate and 1 000 replicates of random taxon addition to search for multiple islands of most-parsimonious (MP) trees. Support for clades was estimated by decay analysis. These decay values were conducted in PAUP* with 100 replicates of random taxon addition on each constraint tree, using command files created in MacClade. The level of homoplasy was summarised by the Consistency Index excluding uninformative characters (CI-u), Retention Index (RI) and Rescaled Consistency Index (RC).

All characters were initially equally weighted so that the greatest degree of congruence between as many characters as possible would distinguish the useful characters from the misleading ones. Once the parsimony analysis was completed, the

Table 2 List of morphological characters used in this study, together with the character states recorded for each character. Characters 2, 14, 16–18, 26 and 52, are overlapping characters that have been converted to non-overlapping character states prior to phylogenetic analyses.

<p>1. habit</p> <ol style="list-style-type: none"> a. herb (or subshrub) b. shrub c. tree <p>2. plant height (non-overlap)</p> <ol style="list-style-type: none"> a. up to 1 m high b. between 1 and 4 m c. more than 4 m <p>The plant height measurements were based on personal field observations, herbarium notes provided by botanical collectors or, less frequently, the measurement of the herbarium specimen when the whole plant was represented by the collection. More commonly, a combination of these data sources was used.</p> <p>3. form</p> <ol style="list-style-type: none"> a. self-supporting (erect or suberect) b. creeping <p>4. epiphyte/hemi-epiphyte</p> <ol style="list-style-type: none"> a. no b. yes <p>5. sexuality</p> <ol style="list-style-type: none"> a. monoecious b. dioecious <p>6. branched hairs</p> <ol style="list-style-type: none"> a. absent b. present <p>7. stinging hairs</p> <ol style="list-style-type: none"> a. absent b. present <p>8. internode</p> <ol style="list-style-type: none"> a. developed (elongate, distinct) b. reduced (not visible) <p>9. stipules</p> <ol style="list-style-type: none"> a. caducous b. persistent <p>10. stipule attachment</p> <ol style="list-style-type: none"> a. free b. connate <p>11. stipule position</p> <ol style="list-style-type: none"> a. lateral (interpetiolar) b. axillary (intrapetiolar) <p>12. leaf arrangement</p> <ol style="list-style-type: none"> a. opposite b. subopposite c. alternate <p>13. leaf petiole</p> <ol style="list-style-type: none"> a. sessile (petiole absent or less than 2 mm long) b. petiolate (petiole at least 2 mm long) <p>14. leaf petiole length (non-overlap)</p> <ol style="list-style-type: none"> a. 0 (absent)–11 mm b. 11–41 mm c. longer than 41 mm <p>15. leaf lobing</p> <ol style="list-style-type: none"> a. not lobed b. lobed <p>16. lamina length (non-overlap): length of lamina, from base to apex</p> <ol style="list-style-type: none"> a. less than 50 mm b. more than 50 mm <p>17. lamina width (non-overlap): width at broadest part of lamina</p> <ol style="list-style-type: none"> a. less than 60 mm b. more than 60 mm <p>18. lamina length: width ratio (non-overlap)</p> <ol style="list-style-type: none"> a. less than 2 b. more than 2 <p>19. lamina symmetry: width comparison</p> <ol style="list-style-type: none"> a. unequal b. equal <p>This character compares the width of the lamina on each side of central axis (often midvein). The comparison is made in the central 1/3 of the lamina. Leaves are regarded as having an asymmetric lamina (hence, unequal) if the width of broadest side is at least 1.34 times the width of the narrowest side. Leaves with equally symmetric laminas (equal) have a 'width' ratio of less than 1.34. Aniso-</p>	<p>phyly and leaf lamina asymmetry are frequently associated (Dengler 1999). Leaf asymmetry is often present in the <i>Urticaceae</i>; in some species it is subtle, whereas in others the leaf lamina is distinctly asymmetric. All species of <i>Elatostema</i> are characterised by having strongly asymmetric (unequal) leaf laminas.</p> <p>20. leaf base</p> <ol style="list-style-type: none"> a. equal b. oblique <p>21. leaf margin</p> <ol style="list-style-type: none"> a. entire b. toothed c. half entire, half toothed <p>22. leaf margin indumentum</p> <ol style="list-style-type: none"> a. glabrous b. hairy <p>23. leaf apex</p> <ol style="list-style-type: none"> a. acute (length < 1.5 times width) b. acuminate (length at least 1.5 times width) <p>24. leaf texture</p> <ol style="list-style-type: none"> a. rugose b. not rugose <p>25. veins number (pairs: non-overlap)</p> <ol style="list-style-type: none"> a. less than 9 b. more than 9 <p>The number of veins in the wider part of the lamina is used when the number of veins on each side of the central axis is unequal. Therefore, the number of veins is not always in pairs.</p> <p>26. venation arrangement</p> <ol style="list-style-type: none"> a. pinnate b. actinodromous c. acrodromous <p>27. venation symmetry – basal secondary veins</p> <ol style="list-style-type: none"> a. both directed towards apex (or almost so) b. both directed towards margin (or almost so) c. one towards apex or almost so, the other towards margin or almost so <p>28. veins – basal secondary pair origin</p> <ol style="list-style-type: none"> a. arises at base of primary vein (or arising at a point < 2mm above base) b. arises above base of primary vein (at least 2 mm above base) <p>29. veins – basal secondary pair distance</p> <ol style="list-style-type: none"> a. basal pair of secondary veins arise together from same position or within 2 mm of each other b. basal pair of secondary veins arise from different positions, at least more than 2 mm apart <p>30. veins – secondary arrangement</p> <ol style="list-style-type: none"> a. joined to next distal secondary vein b. directed to margin or almost so, not joined up to next secondary vein c. some secondary veins directed to margin, others joining up to next secondary vein <p>31. leaf cystolith shape</p> <ol style="list-style-type: none"> a. punctiform b. linear <p>32. leaf abaxial cystoliths venation</p> <ol style="list-style-type: none"> a. absent (cystoliths not arranged on veins of abaxial surface) b. on primary and secondary veins (cystoliths present on primary and secondary veins of abaxial surface) <p>33. leaf abaxial cystoliths interstices</p> <ol style="list-style-type: none"> a. absent (cystoliths not present on interstices of abaxial surface) b. on interstices (cystoliths present on interstices of abaxial surface) <p>34. leaf adaxial cystoliths venation</p> <ol style="list-style-type: none"> a. absent (cystoliths not arranged on veins of adaxial surface) b. present (cystoliths present on veins of adaxial surface) <p>35. leaf adaxial cystoliths interstices</p> <ol style="list-style-type: none"> a. absent (cystoliths not present on interstices of adaxial surface) b. present (cystoliths present on interstices of adaxial surface) <p>36. leaf abaxial indumentum venation</p> <ol style="list-style-type: none"> a. absent (hairs absent from veins of abaxial surface) b. on primary, secondary and tertiary veins <p>37. leaf abaxial indumentum interstices</p> <ol style="list-style-type: none"> a. absent (hairs absent from interstices of abaxial surface) b. on interstices
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Table 2 (cont.)

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| <p>38. leaf adaxial indumentum venation
a. absent (hairs absent from veins of adaxial surface)
b. on primary, secondary and tertiary veins</p> <p>39. leaf adaxial indumentum interstices
a. absent (hairs absent from interstices of adaxial surface)
b. on interstices</p> <p>40. nanophyll (small leaves)
a. absent
b. present</p> <p>41. flower sexuality
a. unisexual
b. bisexual</p> <p>42. male inflorescence
a. sessile (or subsessile)
b. pedunculate (distinctly so)</p> <p>43. male inflorescence density
a. condensed/crowded (male flowers crowded together)
b. open (male flowers spaced from each other)</p> <p>44. male inflorescence branching
a. branched
b. unbranched</p> <p>45. male inflorescence type
a. head-like
b. discoid
c. paniculate
d. racemose
e. spike-like</p> <p>46. male inflorescence involucre bracts
a. absent
b. present</p> <p>47. male inflorescence bracts appendage
a. absent
b. present</p> <p>48. male inflorescence bract margin (when bracts present)
a. glabrous
b. hairy</p> <p>49. male inflorescence order
a. unordered
b. distinctly ordered into compartments</p> <p>50. male flower symmetry
a. actinomorphic
b. zygomorphic</p> <p>51. male flower tepal length (non-overlap)
a. less than 1.8 mm
b. more than 1.8 mm</p> <p>52. male flower tepal number
a. one
b. two
c. three
d. four
e. five</p> <p>53. male flower tepal fusion
a. free (tepals not joined to each other)
b. connate (at least connate on basal half)</p> <p>54. male flower tepal appendage
a. absent (or present as a slightly raised bump)
b. short (less than 0.25 times length of tepal)
c. long (0.25–0.5 times length of tepal)
d. very long (more than 0.5 times length of tepal)</p> <p>55. male flower tepal indumentum
a. glabrous
b. hairy</p> <p>56. male flower stamen number
a. one
b. two
c. three
d. four
e. five</p> <p>57. male flower staminal inflexion in bud
a. inflexed
b. erect</p> | <p>58. male flower rudimentary ovary
a. absent
b. present</p> <p>59. female inflorescence
a. sessile
b. pedunculate</p> <p>60. female inflorescence branching
a. unbranched
b. branched</p> <p>61. female inflorescence arrangement
a. open (female flowers spaced from each other)
b. condensed, crowded (female flowers crowded together)</p> <p>62. female inflorescence type
a. head-like
b. discoid
c. paniculate
d. racemose
e. spike-like</p> <p>63. female inflorescence involucre bracts
a. absent
b. present</p> <p>64. female inflorescence bracts appendage (when bracts present)
a. absent
b. present</p> <p>65. female flower bract margin (when bracts present)
a. absent
b. present</p> <p>66. female flower symmetry
a. actinomorphic (or slightly asymmetrical)
b. zygomorphic</p> <p>67. female flower tepal number
a. zero (tepals absent or tepals minute and so not readily visible)
b. one
c. two
d. three
e. four
f. five
g. six</p> <p>68. female flower tepal comparative size
a. equal
b. unequal</p> <p>69. female flower tepal fusion
a. free
b. connate (at least connate in part)</p> <p>70. female flower staminode presence
a. absent
b. present</p> <p>71. female flower staminode inflexion in bud (when staminodes present)
a. inflexed
b. erect</p> <p>72. female flower ovary
a. straight
b. oblique</p> <p>73. female flower style
a. absent
b. present</p> <p>74. female flower stigma
a. capitate
b. penicillate
c. peltate
d. oblong, filiform to linear</p> <p>75. achene covered by perianth or involucre
a. not enclosed (or only partly so)
b. enclosed (or almost completely so)</p> <p>76. achene surface
a. smooth
b. ribbed
c. dimpled</p> |
|---|--|
-

characters were a posteriori re-weighted according to their RC and, for comparison, their CI-u values, such that those characters with a higher 'parsimony fit' to a tree received a higher weighting than those with lower values. Subsequent analyses using CI-u and RC-weighted characters were conducted with branch-swapping limited to a maximum of 200 trees per replicate and 100 random taxon addition to search for multiple islands of most-parsimonious (MP) trees.

Phenetic analysis

Construction of a distance tree using clustering was calculated using the Unweighted Pair Group Method with Arithmetic Mean (UPGMA), producing a tree reflecting the phenotypic similarities between taxa.

RESULTS

The data matrix comprised 76 characters (Table 2) and 55 taxa (Table 3). Analysis using unweighted characters resulted in 13 198 most parsimonious (MP) trees of 390 steps (CI-u = 0.23, RI = 0.63, RC = 0.14).

The strict consensus tree (Fig. 3) is characterised by a large polytomy containing all members but one of the tribe *Elatostemeae*,

with considerable character support (decay +3). *Pilea nummulariifolia* is placed as sister to the remaining taxa in the tribe (decay +2). This refutes the monophyly of *Pilea*, since *P. microphylla* is closer to members of *Elatostema* and *Procris* than it is to *P. nummulariifolia*. Neither of the other two genera appears monophyletic, although the analysis does not refute monophyly in either case. However, apart from *P. reticulatovenosa*, the remainder of *Procris* spp. are placed within a clade (P1; decay +1) indicating they are more closely related to each other than to *Elatostema*. There are two other clades of *Elatostema* species: i) clade E1 contains seven species from the Mt Kinabalu area of Sabah and receives some support (decay +2); ii) clade E2 that includes *E. latifolium* and *E. tsoongii* (decays +1). Relationships between these three clades and the remaining members of the tribe are unresolved. Hence there is no support from the morphological database for any of the generic groupings within *Elatostemeae*. *Pilea* appears polyphyletic, but this estimate of relationships does not refute the monophyly of either *Elatostema* or *Procris*.

Within the non-*Elatostemeae* taxa, *Dendrocnide sinuata* and *D. stimulans* form a strongly supported clade (decay +7) with *Urtica dioica* sister to these two species (decay +1). *Myriocarpa longipes* (*Boehmerieae*) is sister to this latter clade, rather

Table 3 Morphological data matrix of 55 species and 76 characters (as listed in Table 2); '?' represents inapplicable characters or characters not available from specimens used; character state values in parentheses represent multiple character state scores.

<i>Boehmeria calophleba</i>	110000000?	?211010110	1101020000	0000111010	0?????????	???????????	???????????	??????
<i>B. microphylla</i>	1100000010	1010010110	11110200?0	0000111010	0101400?00	?(23)10?(23)110	1400?02010	?11312
<i>Dendrocnide sinuata</i>	220000100?	?212011010	10?1101000	011111110	011020????	03001311??	???????????	??????
<i>D. stimulans</i>	220000100?	?202011110	0011101101	0111101010	01020?????	030013010?	?20??04000	?00300
<i>Elatostema acuminatum</i>	000000000?	?0000(01)0111	0011011000	1000100001	0001110000	0(34)100(34)010?	?010103101?	?00302
<i>E. auriculatifolium</i>	0100000010	100001010?	101102(02)012	1110000001	011011????	040?040?00	100(34)0010??	??111?
<i>E. backeri</i>	0010000010	10?00??(01)01	1111?11010	1010111010	0001011100	?(34)110(34)010?	?1110010101	?00301
<i>E. bullatum</i>	00(01)0000000	1010010101	11(01)0???????	1111101011	011011??10	0300030?01	011?003(01)01	0?????1
<i>E. curtisii</i>	00?000000?	?000010(01)11	2011001111	?110100000	000100?000	141304010?	?00?005010	?00310
<i>E. dallasense</i>	0(01)001000?0	1000010101	1111???????	1111111111	011011??10	030?130?01	011??03101	0?????0
<i>E. flavovirens</i>	00001000?0	10100(01)0101	11(01)1???????	1111101011	0?1011??20	030?230?01	011??03101	0?????1
<i>E. grande</i>	000000000?	?000010101	1111001111	1111111100	0101101000	131?13010?	?110100?01	?00301
<i>E. griffithianum</i>	0000000010	1010010101	1011011110	1000110000	0110201100	040314010?	?000105111	?00302
<i>E. heyneanum</i>	0000000010	10?0000011	??11012002	1111100001	01?1?00000	0410140?11	??000?????	?00?12
<i>E. integrifolium</i>	0(01)0000000?	?000010111	0011011110	1111001000	0001010110	0?????0?0???	???????????	??????
<i>E. kinabaluense</i>	001000000?	?0000001?1	1101011011	1111100000	0???????????	???????????	???????????	??????
<i>E. latifolium</i>	0000000010	101(12)01(01)111	0011012102	1011100000	01?1?00?00	0310?30?1?	??00?04001	?00?02
<i>E. lineolatum</i>	000000000?	?000000111	1011012010	1011100000	000100?000	0(34)100(34)0?0?	???????????	??????
<i>E. macrophyllum</i>	0(01)0000000?	?011011101	1111(01)01110	1111111010	0001101010	03000301??	???????????	??????
<i>E. marillense</i>	000000000?	?01(01)01(01)111	?011012111	1011000000	011020?000	0(34)120(34)0?0?	?00?10?001	?00?02
<i>E. maraiparaense</i>	01111000?0	10100101(01)1	21(01)1001112	?0011(01)1??1	0?1011??00	0(34)0?1(34)0?(01)1	011??0(345)101	0?????1
<i>E. paludosum</i>	0(01)0000000?	?01(01)01(01)111	1010(01)00111	1011100000	0011100010	(01)30003010?	?110000101	?00300
<i>E. papillosum</i>	0?00000010	10000101?1	1111012010	1000111111	0101100010	0???????????	?1101?????1	?00?02
<i>E. parvum</i>	0010000010	1000000(01)01	1111011110	1101100011	0001010100	041114010?	?1110010101	?00301
<i>E. pedunculatum</i>	000000000?	1000010(01)01	1011022110	1000111010	0101011000	131?0301??	???????????	??????
<i>E. pinnatifidum</i>	0(01)00(01)000?0	101001010(01)1	(01)101?0????	111(01)0111111	001001?010	030?130?01	0?1??03(01)01	0?????1
<i>E. purpurascens</i>	000000000?	1010000101	11(01)1???????	1111101011	011001??00	0301?30?01	011??03001	0?????1
<i>E. repens</i>	0010000010	1000010111	0001010110	1000111000	011020?000	14100401??	???????????	??????
<i>E. reticulatum</i>	0(01)0000000?	?000010101	1111011111	1011111000	0101111000	(01)41114010?	?111000?10	?00300
<i>E. rostratum</i>	0(01)0000000?	?000010111	2111011110	1111111100	0001011100	041214010?	?1110010101	?00301
<i>E. serpentinicola</i>	00001000?0	10000(01)0101	??(01)1???????	111111(01)111	011011????	030?031?01	0111?0(34)001	0?????1
<i>E. sessile</i>	000000000?	?000010111	1111011110	1011111010	0???????????	???????????	???????????	??????
<i>E. sinuatum</i>	000000000?	?00001(01)1?1	2011001111	1010100001	0???????????	???????????	?00?005001	?00?10
<i>E. stipitatum</i>	0010000010	1000010(01)01	1101011111	1101111010	0101011100	031213011?	?111100?01	?00300
<i>E. strigosum</i>	000000000?	?0000101?1	1111011110	1010111010	0001111000	(01)(34)121(34)010?	?1110010101	?00301
<i>E. tsoongii</i>	0000000010	1012010111	00010120?2	1011100000	0???????????	???????????	?30?004?01	?00?0?
<i>E. urvilleanum</i>	0010000000	100000(01)101	2011011110	1010100010	0001011110	031203010?	?111100?01	?00301
<i>E. velutinicaule</i>	0010000000	12000001?1	1001001011	1010111010	0001001000	131213010?	?001100?01	?0030?
<i>Elatostema</i> sp.A399068	0000000010	1000000001	1000011000	1010000010	0???????????	???????????	?111000?01	?00301
<i>Myriocarpa longipes</i>	210000000?	?212011010	11?1001001	1000111010	01?1400100	03?01301??	???????????	??????
<i>Parietaria judaica</i>	000000000?	?211000(01)10	011021111	0000111010	0001000100	(01)31013010?	?000104010	?00?10
<i>Pilea microphylla</i>	0010000010	1010000011	0001001111	1000111000	0010200000	131003010?	?200030101	?00310
<i>Pl. nummulariifolia</i>	0010000010	1011000010	10?0020000	1111111110	0001000100	131213011?	?200103101	?00300
<i>Procris anfracta</i>	0(01)01100001	111(01)010101	000?0011??	10010000??	0???????????	???????????	?00?00????	?0?010
<i>Pr. archboldiana</i>	000?100000	1110010101	(01)001001100	0111100001	01102?0000	0400?04111	000000??01	000010
<i>Pr. frutescens</i>	0001000000	1110010111	1110(01)01101	1111100001	0110200000	0(34)000(34)0101	00000050?0	000012
<i>Pr. goepeliana</i>	0(01)000000000	101(01)010111	0001001000	1010100001	0110200000	0400040111	001???????	??????
<i>Pr. insularis</i>	000000000?	?010010111	001100110(01)	1111100001	011020??00	1410040001	00?000?0?1	000010
<i>Pr. pedunculata</i>	0(01)01000000	1110010111	001?001111	1111100001	0110200000	1400040101	100?00?0?0	?00010
<i>Pr. reticulatovenosa</i>	1001000000	1100010111	201?0011?1	1110000001	0???????????	???????????	?0?????????	??????
<i>Pr. ruhlantii</i>	0(01)01000000	1110010111	00110011?1	1111100000	0???????????	???????????	???????????	??????
<i>Pr. urdanetensis</i>	0101000000	1110000111	201?0011?1	1111100000	01102?????	???????????	?0?????????	??????
<i>Pr. wightiana</i>	?(01)??000001	?110010111	?11?00?0???	111110000?	01?????????	???????????	???????????	?0?????
<i>Urtica dioica</i>	0(01)0000100?	?1110(01)0010	11000110?1	0001111010	011020??00	031013011?	?20?004100	?00010
<i>U. urens</i>	000000100?	?01(01)000010	1101020001	0000111010	0001000100	(01)310130?01	1000104100	?00310

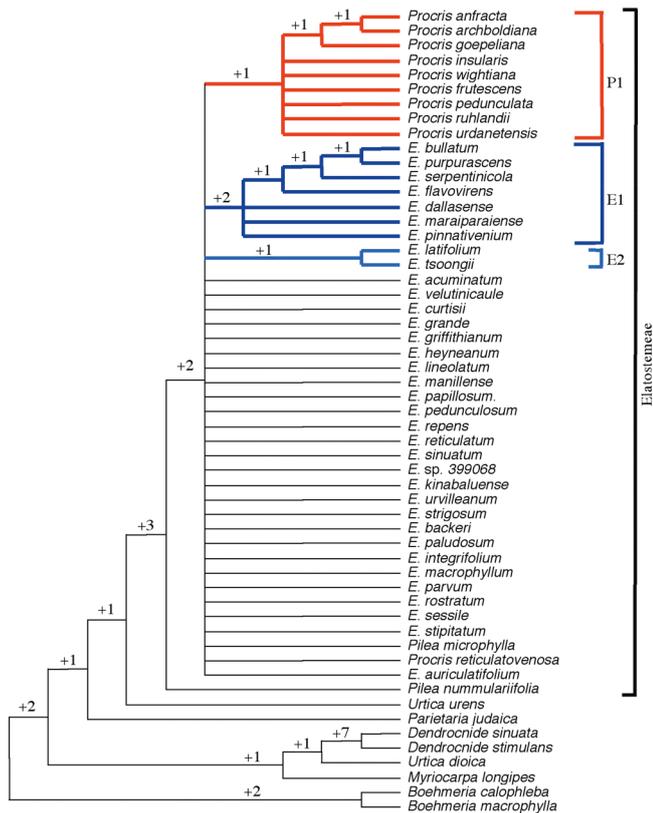


Fig. 3 Strict consensus tree obtained from a heuristic search with 1 000 replicates of the equally weighted morphological dataset; tree length = 390 steps; RI = 0. 63; RC = 0.14 coloured lines indicate the clades referred to in text: blue lines = *Elatostema bullatum* clade (E1), pale blue lines = *E. latifolium*–*E. tsoongii* clade (E2), red lines = *Procris* p.p.maj. clade (P1). Decay values are cited above the lines.

than being placed with the two species of *Boehmeria*. Tribe *Urticeae* appears polyphyletic because *Urtica urens* is placed closer to *Elatostemeae* than to the *Dendrocnide*–*Urtica dioica* clade. *Parietaria judaica* (*Parietarieae*) is sister to the *Urtica urens*–*Elatostemeae* clade (decay +1).

Since the strict consensus tree was poorly resolved, the majority rule tree (Fig. 4) was considered because it may provide additional information on potential relationships. *Procris reticulatovenosa* is placed sister to all other *Procris* spp. (clade P1) in 55 % of trees, suggesting that *Procris* may be monophyletic. *Elatostema curtisii* and *E. sinuatum* are grouped together with all *Procris* species (in 94 % of the trees) forming a clade P2. There is a suggestion (in 80 % of the trees) that clade P2 and several other members of *Elatostema*, namely members of subg. *Pellionia*, *E. manillense* (subg. *Elatostematoides*) and *E. auriculatifolium* (either a member of subg. *Elatostema* or subg. *Pellionia*), plus *Pilea microphylla*, are closely related to each other and forming a clade (P3).

Within *Elatostema* species, *E. macrophyllum* and *E. paludosum* (both subg. *Elatostema*) group together in 62 % of the trees (clade E3), with this clade sister to several other members of subg. *Elatostema* (clade E1) in 62 % of the trees. Clade E4, comprising members of subgenera *Elatostema*, *Elatostematoides* and *Weddellia* (in 57 % of the trees), and *E. acuminatum* and *E. integrifolium* occur together in 74 % of the MP trees (clade E5).

The UPGMA dendrogram (Fig. 5) recognises two major morphological groups (A and B) and several minor ones. Group D1 comprises all the species grouped in clade E3 (Fig. 4) plus five other species that are unresolved in Fig. 4. Group D2 consists of the clade E1 (Fig. 3, 4), E3 (Fig. 4), and *E. papillosum*. Group B

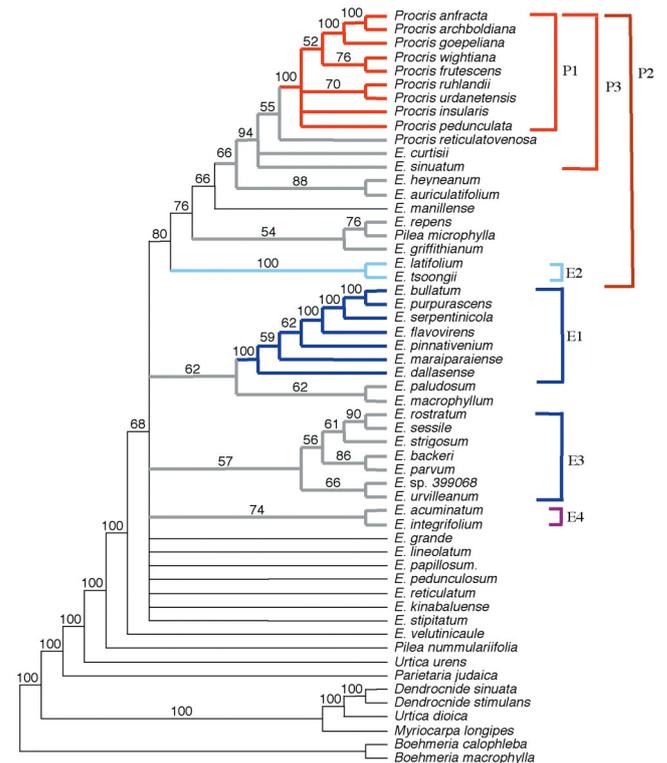


Fig. 4 Majority rule tree, equally weighted morphological dataset; percentage of MP trees supporting each node is given above the line; grey lines = new clades formed on this cladogram that were not resolved on strict consensus tree (Fig. 3); other coloured lines refer to clades recognised in strict consensus tree (refer Fig. 3 for explanation).

shows a close similarity to clade P3 (Fig. 4), containing all the taxa in the latter, plus clade E5 (Fig. 4) and two additional species, *E. kinabaluense* and *E. lineolatum*.

Pilea nummulariifolia clusters with species of the *Boehmerieae*, *Urtica* and *Parietaria judaica*. Species of *Urtica* are clustered with *Parietaria judaica* rather than with species of *Dendrocnide*. *Myriocarpa longipes* is clustered with species of *Boehmeria* rather than with *Dendrocnide*–*Urtica dioica* (*Urticeae*) as suggested by the parsimony analysis (Fig. 3). Hence the UPGMA analysis supports the current circumscription of *Boehmerieae* (based on species included in this study), but does not support the *Urticeae*.

Analysis of CI-u weighted data found 16 trees (RI = 0.69, RC = 0.22). The strict consensus tree of these (Fig. 6) shows much better resolution of relationships between species than the equally weighted one. It contains a number of clades that are similar to groups in the UPGMA analysis. Within the *Elatostemeae* there are two main clades labelled A and B (Fig. 6). Within clade A there are two terminal subclades that are similar to group A of the UPGMA analysis (Fig. 5), namely E1* and E4*. The topology and composition of the upper subclade (E4*) is similar to group D1 (Fig. 5) and also to clade E4 (Fig. 4) (containing all members of the latter plus three additional species, *E. pedunculatum*, *E. reticulatum* and *E. stipitatum*). The lower subclade (E1*) comprises clade E1 (as resolved in Fig. 3) plus *E. macrophyllum*, and also with some species common with that of group D2 (Fig. 5). Likewise, the species composition of clade B (Fig. 6) is similar to clade B (Fig. 5), as well as to some elements in Fig. 3 and 4. All species of *Procris* are grouped within the terminal polytomy (P1*) of clade B (Fig. 6), with *Procris reticulatovenosa* nested among members of *Procris* pro parte majore clade (P1 of Fig. 3), and *E. curtisii*–*E. sinuatum* clade sister to this (also refer Fig. 4, 5). All the remaining eight taxa that attach to the base of the *Procris*

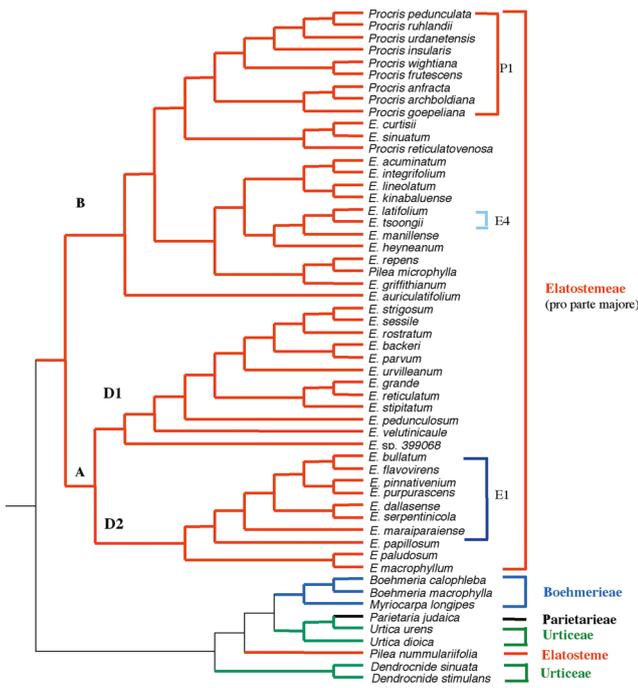


Fig. 5 UPGMA tree of equally weighted morphological dataset (refer Fig. 3 for further details); coloured lines and text are used to make it easier to distinguish the tribal groupings sensu Gaudichaud (1830) and Friis (1993). **A, B, D1** and **D2** = clades as referred to in text.

clade in Fig. 4, and are also placed within clade B (Fig. 5), are attached at the base of clade B in Fig. 6. Hence, there is considerable similarity in the estimates of relationships and degree of similarity within the ingroup taxa from all three methods of analysis. Tribe *Urticeae* is polyphyletic in the CI-u weighted analysis, with *Urtica urens* placed outside the *Urticeae* clade and closer to *Elatostemeae*, as also shown in the parsimony analysis of the equally weighted dataset (Fig. 3, 4). However, *Myriocarpa longipes* (*Boehmerieae*) is nested within the main *Urticeae* clade (Fig. 6), or is placed sister to the main *Urticeae* clade (Fig. 3, 4). Hence neither analysis provides support for the inclusion of *Myriocarpa longipes* within *Boehmerieae*. Analysis of RC-weighted data (not presented here) found 71 trees of 60.80 steps (RI = 0.75, RC = 0.27). The topology of the strict consensus tree of the RC-weighted data was topologically similar to the CI-u weighted strict consensus tree.

DISCUSSION

The low level of decay support for the clades within the equally weighted strict consensus tree indicates the weakness of the traditionally used morphological characters for indicating evolutionary affinities (Fig. 3). Even though there are several robustly supported clades in the strict consensus trees from the equally and CI-u weighted characters (Fig. 3 and 6, respectively), the RC-weighted tree (not presented here) and in the majority rule tree from the equally weighted analysis (Fig. 4), most of these branches are only supported by one or two character changes as shown in the phylogram of one of the MP trees from the equally weighted analysis (Fig. 7).

Evaluation of the subgeneric classification of Schröter & Winkler

The previous subgeneric classification of Schröter & Winkler (1935, 1936) is mapped onto the strict consensus trees of equally weighted (Fig. 8) and the CI-u weighted morphological analyses (Fig. 9). The following species, *E. auriculatifolium*, *E. bullatum*, *E. dallasense*, *E. flavovirens*, *E. maraiparaiense*, *E. pinna-*

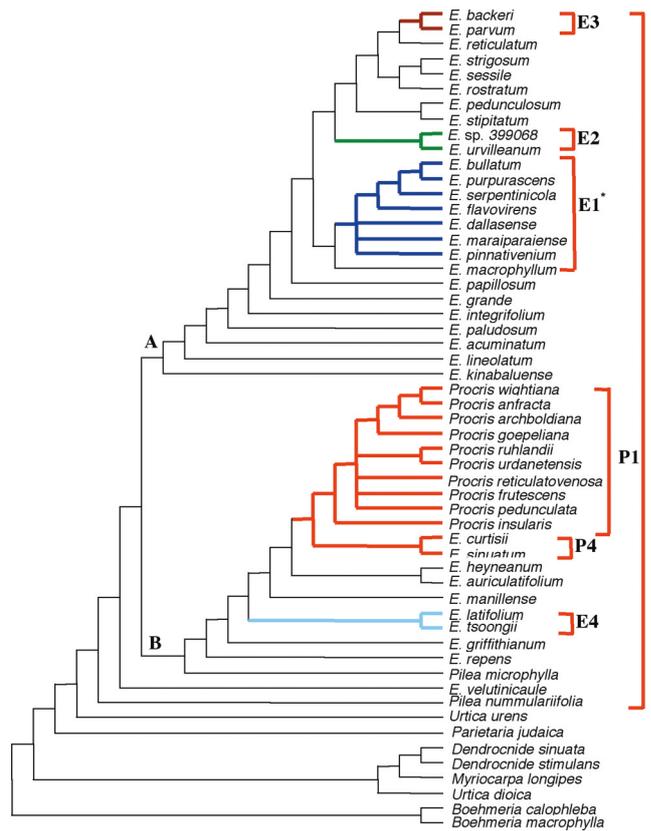


Fig. 6 Strict consensus of 16 MP trees obtained from heuristic searching of the CI weighted morphological dataset; tree length = 89; RI = 0.69; RC = 0.22; coloured lines indicate clades that are also formed on the strict consensus of the equally weighted data (Fig. 3); labelled clades as referred to in the text.

venium, *E. purpurascens* and *E. serpentinicola* have been here assigned to subgenera based on an examination of descriptions (Beaman & Cellinese 2004) and photographs of herbarium specimens (held at L) determined by R.S. Beaman. However, the subgeneric position of *E. auriculatifolium* is unclear because although the description suggests that this species may be a member of subg. *Elatostema*, based on the photograph of J. & M.S. Clemens 50984, (L565832 – possibly with male flowers) this species could belong to either subg. *Elatostema* or subg. *Pellionia*. *Procris*, recognised as a distinct genus by Schröter & Winkler (1935, 1936), has been included here for comparison. The lack of resolution in the equally weighted analysis means that there is little information relevant to the subgeneric concepts. All but one representative of *Procris* are grouped in clade P1, but the representatives of subg. *Elatostema*, *Elatostematoides*, *Pellionia* and *Weddellia* are placed within the large polytomy. Hence the analysis neither supports nor refutes Schröter & Winkler’s groupings. Comparison of the subgeneric classification with the re-weighted analysis is more fruitful (Fig. 9). All representatives of *Procris* are placed within clade P1*, and all representatives of subg. *Pellionia* attach as a grade below P1* within clade B, along with *E. manillense* (subg. *Elatostematoides*). Therefore, these data support the strong affinities of subg. *Pellionia* and *Procris*. Furthermore, these morphological data support the reduction of *Procris* to an infra-generic level within *Elatostema* as suggested by Hallier (1896). The two representatives of subg. *Elatostematoides* are widely separated within both clade A (*E. rostratum*) and clade B (*E. manillense*); there is no evidence of them being close relatives. The three species of subg. *Weddellia* (*E. backeri*, *E. parvum* and *E. papillosum*) are placed within clade A, but only two of these species (*E. backeri* and *E. parvum*) are grouped

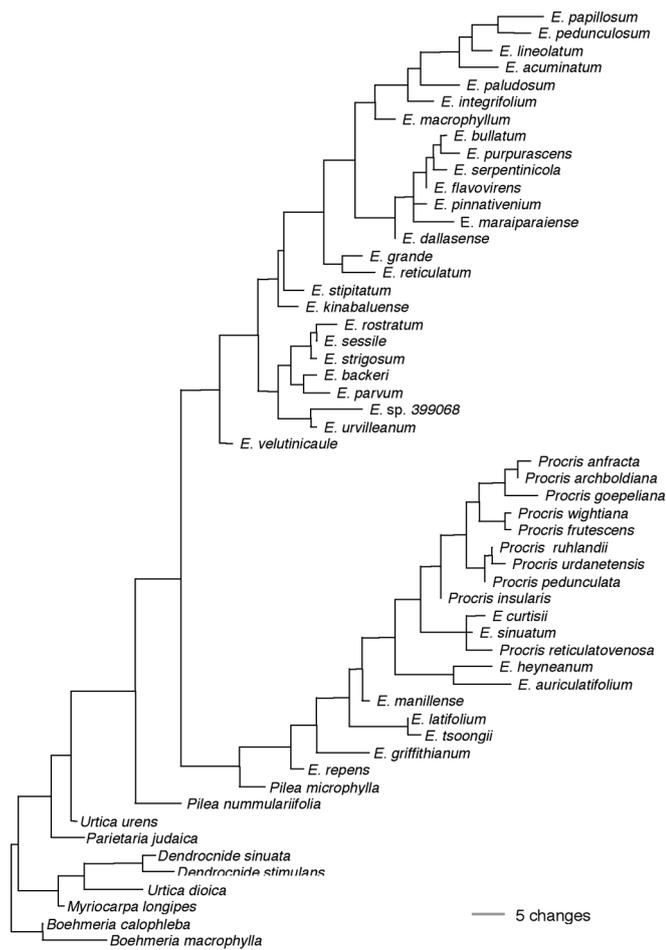


Fig. 7 Phylogram (branch lengths proportional to amount of change) of one of the MP trees found from the parsimony analysis of the equally weighted morphological dataset.

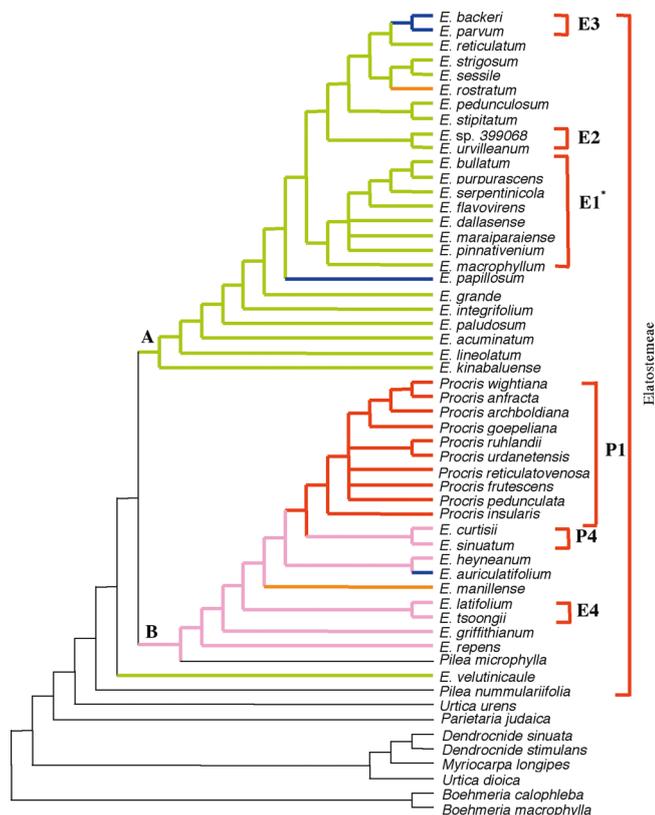


Fig. 9 Subgeneric classification (sensu Schröter & Winkler 1935, 1936) mapped on the strict consensus tree of CI weighted morphological dataset. Details of coloured lines are given in Fig. 8.

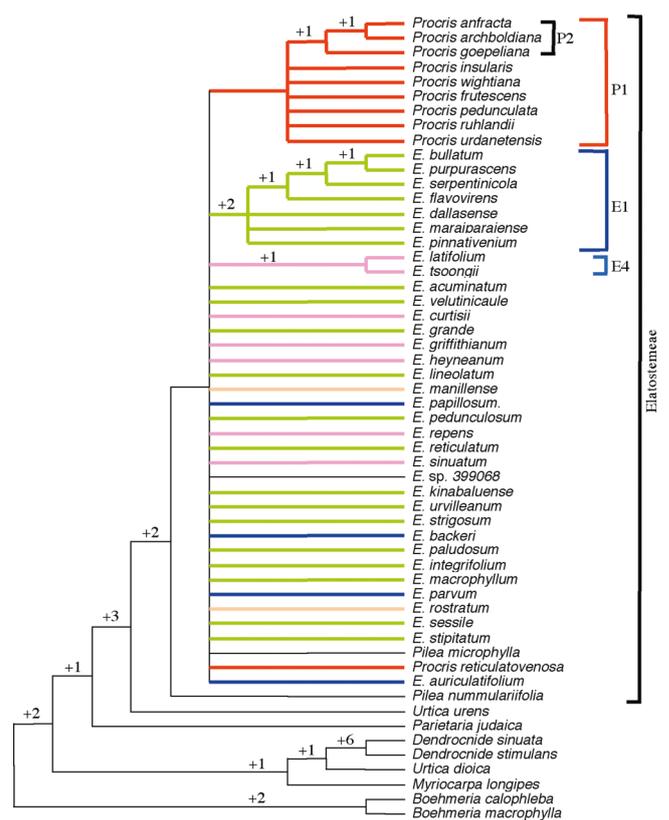


Fig. 8 Subgeneric classification (Schröter & Winkler 1935, 1936) mapped on the strict consensus tree of equally weighted morphological dataset. Pink lines = subg. *Pellionia*; gold lines = subg. *Elatostematoides*; blue lines = subg. *Weddellia*; green lines = subg. *Elatostema*; narrow black line = not assigned to subgenus; red lines = a currently separated genus *Procris*. Decay values are cited above lines.

together, and these appear to be more closely related to species of subg. *Elatostema* than to the other species of subg. *Weddellia*. All members of subg. *Elatostema* are placed within clade A, except *E. velutinicaule*, which is placed at the base of the *Elatostemeae*-clade.

The inclusion of *Pilea microphylla* within the representatives of *Elatostema* in all analyses of the morphological data (Fig. 3–9) does not support the monophyly of *Pilea*. However, a larger sample of species of *Pilea* and an expanded character-set are required before the phylogeny of this genus could be resolved.

CONCLUSION

Parsimony analysis of the equally weighted morphological dataset provided very little resolution of relationships within *Elatostema*–*Procris*. The fit of the data to the resultant MP trees was very low (RC = 0.14), indicating a very high level of homoplasy in many characters. Parsimony analysis with re-weighted characters greatly improved the resolution (Fig. 6). We conclude that the groupings obtained from the CI-u and RC-weighted parsimony analyses indicate the existence of some phylogenetic signal in these data, although this is weak and mostly obscured in the equally weighted parsimony analysis.

Based on the analyses of these morphological data, there is no support for the subgeneric classification of *Elatostema* by Schröter & Winkler (1935). The more recent infrageneric classification of *Elatostema* by Wang (1980a) into sections and series, has not been considered here. However, since Wang (1980a) more or less maintained the same taxonomic concepts as Schröter & Winkler's infrageneric classification, but

regarded their subgenera as sections, there is no support for his sect. *Elatostema* or sect. *Weddellia*. Since the monophyly of *Elatostema* subg. *Pellionia* is not supported in our analyses, the recognition of this taxon, but as the distinct genus *Pellionia* (Wang 1980b), is also not supported by the morphological data used here. Therefore, at least in part, there is no support for the sectional and generic classification of these above taxa as defined by Wang (1980a, b). Furthermore, based on the morphological characters analysed here, the taxonomic status of *Pilea* and *Procris* requires further review. A re-assessment of morphological characters and consideration of additional morphological features would be useful. It is recommended that the usefulness of morphological characters in evaluating the phylogeny of infra-generic taxa of *Elatostema*, together with those of other *Elatostemeae*, would greatly benefit from being considered within a molecular framework based on analyses of molecular data. Since greater homoplasy is often found in morphological data (Givnish & Sytsma 1997a), morphological data may be misleading compared to the large statistical advantage of molecular data (Givnish & Sytsma 1997b). Studies based on molecular data are more likely than morphological studies to provide accurate insights into phylogenetic relationships.

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